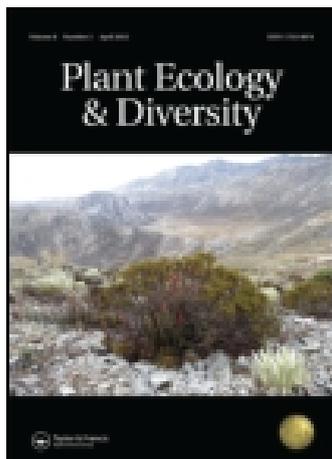


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Soil nutrient availability determines the facilitative effects of cushion plants on other plant species at high elevations in the south-eastern Himalayas

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Background: Cushions are the typical nurse species of high-elevation environments. However, few studies have explored the differences in facilitative power and environmental amelioration between nurse plants of different species that share a common cushion morphology.

Aims: To compare the nurse effects of different alpine cushion plants and their mechanism.

Methods: We compared the effects of two co-occurring cushion species, *Potentilla articulata* and *Arenaria polytrichoides* on species richness, Shannon–Wiener diversity and the evenness of vascular plant assemblages in the Himalayas. In addition, we compared the temperature and the soil nutrients within and outside the two cushion species.

Results: The presence of either cushion species significantly increased the species richness and diversity in comparison with the areas outside the cushions; *P. articulata* cushions were associated with greater species richness than *A. polytrichoides*. Substrate temperatures were similar under the two species and in open areas, but nitrogen and potassium levels were higher under either of the two cushion species than they were outside. Soil phosphorus and potassium concentrations were significantly higher beneath *P. articulata* than beneath the *A. polytrichoides* cushions.

Conclusions: Our results indicate that facilitation of local species richness by cushion plants contributes to the structure of the alpine plant community in the eastern Himalayas. The intensity of the nurse effect varies with the soil nutrient level beneath different benefactor species.

Keywords: alpine environment; *Arenaria polytrichoides*; cushion plant; Himalaya; facilitation; *Potentilla articulata*

Introduction

The stress gradient hypothesis (SGH) predicts that the relative incidence of facilitation or competition will vary inversely across gradients of physical stress or ecosystem productivity, positive interactions increasing with physical environmental harshness (Bertness and Callaway 1994; Maestre et al. 2009). Alpine habitats are well known for their stressful environmental conditions (Körner 2003) and, consistent with the SGH, studies conducted during recent decades have shown that the presence of neighbours enhances both the distribution and the abundance of many species in high-elevation communities, indicating that the interactions in these habitats are predominately facilitative (e.g. Choler et al. 2001; Callaway et al. 2002; Cavieres and Badano 2009). At many such sites the positive interactions involve nurse plants that facilitate the establishment of other species within their canopy, since they offer microhabitats that are more favourable for seed germination and/or seedling recruitment than the surrounding environment (Cavieres et al. 2006, 2007). The facilitative effects of nurse plants typically include the dampening of extreme temperatures, together with increases in soil moisture and nutrient availability (Callaway 2007).

As one of the conspicuous life forms in the most exposed alpine habitats, cushion plants are known to modify the physical environment as a result of their low stature and compact form (Arroyo et al. 2003; Körner 2003; Cavieres et al. 2007; Yang et al. 2010). Cushion plants may therefore function as nurses, allowing non-cushion species to establish and survive within their canopy (Franco and Nobel 1988; Callaway and Walker 1997). This hypothesis is supported by studies covering a wide range of alpine conditions (e.g. Cavieres and Badano 2009; Badano et al. 2010; Yang et al. 2010). However, although there are many general descriptions of facilitation by cushion plants, few studies have examined the ways in which different cushion species affect their environment or have tested the variations in the effect of different species of similar cushion morphology (but see Badano and Cavieres 2006a; Cavieres et al. 2007, 2008). Evidence from the central Chilean Andes, which has a typical Mediterranean climate, indicates that cushion plants do in general act as nurses, but that their specific effects vary between species (Badano and Cavieres 2006a). Cavieres et al. (2008) showed that the facilitative effect of two cushion species (*Laretia acaulis* and *Azorella*

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monantha) on the establishment and performance of a non-native species (*Taraxacum officinale*) was different, due to differences in the soil nutrients beneath the cushions.

As happens in other mountain areas, many phylogenetically distant plant species, such as *Chinocharis hookeri* (Boraginaceae), *Arenaria polytrichoides*, *A. bryophylla* (Caryophyllaceae), *Androsace tapete* (Primulaceae) and *Potentilla articulata* (Rosaceae), exhibit cushion morphology at high elevations in the south-eastern Himalayas. The role of cushion species as nurse plants in this region has recently received attention (Yang et al. 2010; de Bello et al. 2011; Dvorský et al. 2013). In the south-eastern Himalayas, Yang et al. (2010) has shown that the facilitative effect of *A. polytrichoides* cushions on other plant species was the result of improved nutrient availability, which increased with elevation. In contrast, de Bello et al. (2011) and Dvorský et al. (2013) found no facilitative effect of cushion species on other plant species at high elevations (ca. 5900 m) and under extremely dry conditions (rainfall <100 mm year⁻¹) in the north-western Himalayas and in the Trans-Himalayan region. The findings of Yang et al. (2010), de Bello et al. (2011) and Dvorský et al. (2013) highlight the importance of abiotic factors in the interaction between cushion plants and other plant species. However, the differences in microclimatic conditions within cushions and their impact on the interaction between species is still unclear in this region.

In the present study we examined the effect of two co-occurring cushion species, *Potentilla articulata* (Rosaceae) and *Arenaria polytrichoides* (Caryophyllaceae) (Figure 1(a)) on plant community species richness (*S*), diversity (*H'*) and evenness (*J*) in an alpine ecosystem in the south-eastern Himalayas. In order to gain an insight into the mechanisms involved in any facilitation that might be occurring, we also measured temperature and nutrient concentrations in the soil beneath and outside cushions of both species. In this study we hypothesised (1) that both cushion species should act as nurse species and

locally increase species richness and diversity, and thus decrease the evenness of the alpine plant community studied, and (2) that the magnitude of the effect would be related to the extent to which the surrounding environment was modified by the presence of the two cushion species.

Materials and methods

Study species

Potentilla articulata Franchet (Rosaceae) is a species that forms tight hemispherical cushions in high alpine habitats in the south-eastern Himalayas (Figure 1(b)). Its vegetative growth usually begins in early June and it flowers from mid-July to early August (the authors' personal observations).

The genus *Arenaria* (Caryophyllaceae) is mainly found in temperate to arctic regions and contains more than 300 species in 10 subgenera. *A. polytrichoides* Edgeworth (subgenus *Eremogone*), is a long-lived perennial herb that forms hemispherical cushions and is mainly found at high elevations in the south-eastern Himalayan region (Figure 1(c)). Vegetative growth of this plant starts as soon as the snow cover disappears, and flowering occurs from late May to early June (the authors' personal observations).

Study site

The study site was located at an elevation of 4700 m at the Lakaka Pass on Baima Snow Mountain, Deqen County, Yunnan Province, south-west China (28° 20' N, 99° 05' E, Figure 2), where the two target cushion species co-occur. This site was chosen due to its accessibility, and also because facilitation by *A. polytrichoides* cushions has already been shown to be frequent and important in the plant community (Yang et al. 2010). The study site consisted of alpine scree in which cushion plants occupied discrete patches, separated by large open areas mainly composed of rocks and screes. Although cushions were the most conspicuous growth form at the sampling site, a number of perennial alpine herbs and prostrate shrubs were also present, including *Saussurea velutina*, *S. pachyneura*, *Saxifraga wardii*, *Meconopsis horridula* and *Rhododendron tapetiforme* (the authors' personal observations).

At high elevations in the Sino-Himalayas the summer climate is monsoonal and characterised by cold rain or sleet, interrupted by short periods of intense solar radiation (Yang et al. 2008). Annual precipitation records from 1982 to 1984 at the nearest meteorological station (28° 23' N, 99° 01' E, elevation 4290 m), 10 km from the study site, gave figures of 680–790 mm, with 35, 125 and 550 mm falling in May, June and July–October, respectively. The annual average air temperature is –1.0 °C; the difference in mean monthly temperature between the coldest and warmest months is around 15 °C and the mean wind speed is

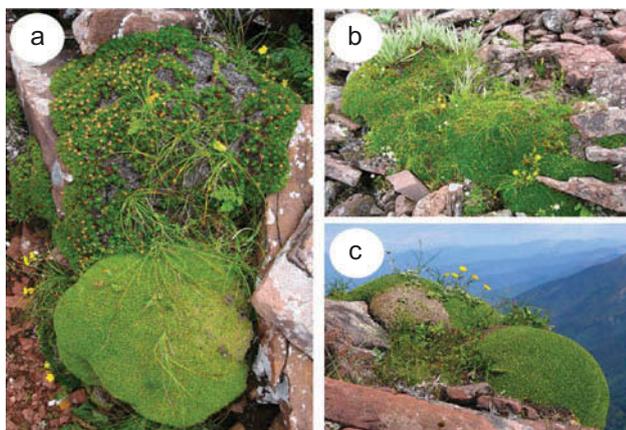


Figure 1. (a) *Potentilla articulata* (upper) and *Arenaria polytrichoides* (lower) cushions co-occurring at 4700 m elevation in the Sino-Himalayas; (b) *Potentilla articulata* cushions; (c) *Arenaria polytrichoides* cushions.

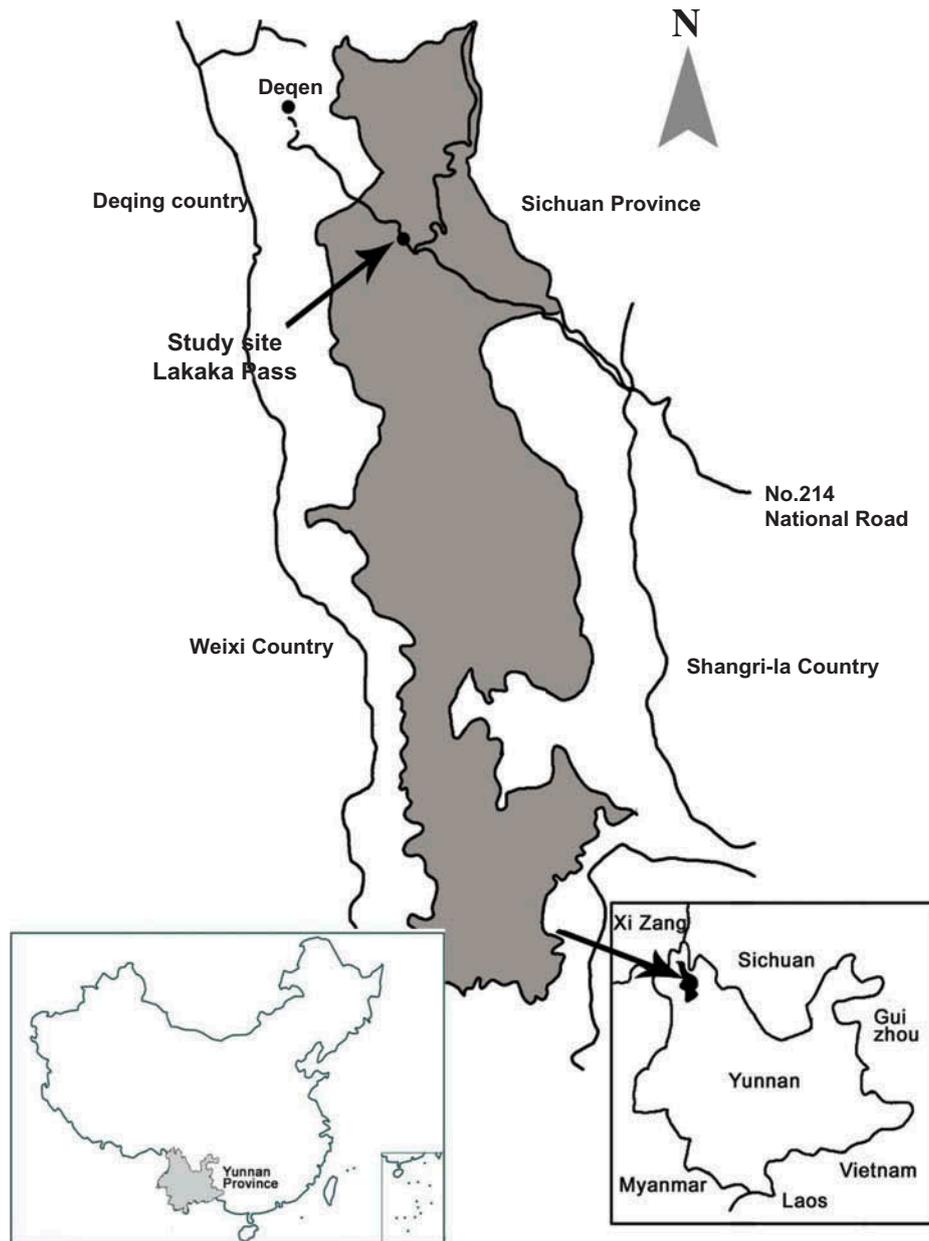


Figure 2. The location of the study region and site (Li 2003). The map at the lower left shows the location of Yunnan Province in China. The map at lower right indicates the study region in Yunnan Province.

$2.9\text{--}3.1\text{ m s}^{-1}$ (Wang 2006). The growing season normally starts in mid-May at snow melt, and ends in mid- to late-September, when the summer monsoon ceases (Yang 2009).

At the study site we recorded air temperature (T_a), ambient solar radiation (I), and relative humidity (RH) ca. 15 cm above soil surface using an integrated thermistor (1400–104 RH/air temperature sensor, LI-COR Inc, Lincoln, NE, USA) and a quantum sensor (Li-190SA, LI-COR Inc), each connected to a data logger (Li-1400, LI-COR Inc). Data were recorded every 5 min during three periods: 25–31 May, 10–16 August and 26 September–2 October 2009, corresponding to the early, middle and late periods of the growing season, respectively (Appendix).

Sampling of species in the cushions and cushion-free areas

At the study site we sampled the two cushions species, *P. articulata* and *A. polytrichoides*, which co-occurred within the same community. Most of the individual cushions of the two species had diameters between 30 cm and 50 cm, and following the protocol suggested by Cavieres and Badano (2009), in the middle of the growing season in mid-August 2009, 50 visibly healthy individuals (without senescing and damaged parts) of each cushion species were randomly selected. All plants growing within the cushions selected were identified to species level and the number of individuals of all occurring species were recorded. Bearing in mind that cushions usually have an elliptical form, we also measured the maximum and

minimum axes of each cushion in order to estimate its surface area. To allow comparison with surrounding cushion-free areas, the shape of each sampled cushion was replicated using a wire frame (with the same diameter as the sampled cushions, between 20 cm and 50 cm). These frames were randomly placed in a cushion-free area at least 1 m from any cushions, and all plant individuals within the wire frames were identified to species level and the number of individuals recorded. Data from the cushions and cushion-free areas were used to estimate species richness, diversity and evenness. This was carried out for all samples, pooling cushion and cushion-free data to estimate the community attributes described below.

Relative effect of the two cushions on species assemblages

We constructed a species accumulation curve for both cushions and cushion-free areas, following the protocol suggested by Cavieres and Badano (2009). In such analyses, the point along the sampling effort axis where the species accumulation curve reaches an asymptote indicates the number of samples needed to successfully sample the full assemblage of species (Gotelli and Colwell 2001). For this we generated a species \times samples matrix for each habitat type, in which each cell (i, j) indicated the presence (1) or absence (0) of the i th species in the j th sample (Cavieres and Badano 2009). From these matrices 500 samples were withdrawn at random, with replacement, for each sample size (ranging from one sample to the maximum number of samples), and the 500 acquired values of species richness were averaged. The average values of species richness were then plotted against the respective sample size to construct a sample-based rarefaction curve for each habitat. All rarefaction analyses were carried out using EstimateS v. 8.02 software (Colwell 2000).

Species richness (S), Shannon–Wiener diversity (H') and evenness (J) at the landscape scale

As cushion patches covered only a small fraction of the habitat, the estimates of S , H' and J for plant assemblages were made after adjusting for the relative cover of the cushions. After recording the cover of cushions and cushion-free areas from 10 parallel line transects (50 m long, and 10 m apart), following Badano and Cavieres (2006a), the average cover of each cushion species was found to be 8.0%. Using 50 samples collected from cushion-free areas we generated a species \times samples matrix, in which each cell (i, j) indicated the abundance of the i th species in the j th sample, and simulated S , H' and J for the plant community without cushions. To estimate S , H' and J for the whole community, including cushions, we generated synthetic data sets combining the data of cushions and cushion-free areas in a single species \times samples matrix and used percentage cover of different habitat types (cushion and cushion-free areas) to weight these data sets (Badano and Cavieres 2006a). For the community that included *P. articulata* or *A. polytrichoides* we simulated plant

assemblages for each cushion species by randomly replacing four samples in the species \times sample matrix constructed for cushion-free areas with four samples from within the cushions. This meant that the synthetic data set included four randomly selected samples from the cushions and 46 randomly selected samples from cushion-free areas. The synthetic complete community samples (cushion + open areas) of the study site therefore occupied the same area, but included 8% cushion patches. For the community that included both *P. articulata* and *A. polytrichoides* we randomly replaced eight samples in the species \times sample matrix constructed for cushion-free areas with eight samples from cushions (four samples from each cushion species), which meant that the synthetic data set included eight randomly selected samples from two cushion species and 42 randomly selected samples from cushion-free areas. To avoid bias due to differences in the samples that were replaced, we simulated the complete communities 20 times with a species \times sample matrix separately for each of the two and with both cushion species, and applied rarefaction analysis to each of these data sets (Badano and Marquet 2008). Species richness (S) and diversity (H') for each rarefaction run were estimated using Coleman's species richness estimator (Coleman et al. 1982) and the Shannon–Wiener diversity index (Magurran 1988). Coleman's species richness hypothesises that the number of species to be found residing in a given region is a random variable whose magnitude depends on the relative area of the region and the overall abundances of the species; details are given in Coleman et al. (1982). 20 values of species richness and diversity were thus averaged and plotted against the respective sample size, and values at the asymptote of the rarefaction curves were considered to give maximum likelihood estimates of species richness and diversity (Badano and Cavieres 2006a, 2006b).

For each sample size, evenness (J) was computed as

$$J_n = H'_n / \ln(S_n) \quad (1)$$

In Eq (1), $\ln(S_n)$ indicates the maximum diversity that communities could attain if all species were equally abundant, and n is the sample size from which values of H' and S were used to calculate evenness (Magurran 1988; Badano and Cavieres 2006a, 2006b). Further, values of S and H' at the asymptote of these rarefaction curves were used to calculate a maximum likelihood estimate of J for both the cushion-free areas and the community including cushions at the study site. The species richness of the community without cushions at the study site was estimated from the asymptotes of the rarefaction curves previously constructed for the cushion-free areas (Badano and Cavieres 2006a). The rarefaction analyses were carried out using EstimateS v. 8.02 software (Colwell 2000), and 95% confidence intervals were calculated to assess whether S and H' at the entire community level differed between the samples taken at the open areas and the synthetic data set.

The effect of the presence of each cushion species on S , H' and J for the entire community was calculated using the methods suggested by Badano and Cavieres (2006a), and we calculated the associated proportional increases for species richness, species diversity and species evenness as follows:

$$[(S_L - S_U) / S_U] \times 100\%, \quad (2)$$

$$[(H'_L - H'_U) / H'_U] \times 100\%, \quad (3)$$

$$\text{and } [(J_L - J_U) / J_U] \times 100\%, \quad (4)$$

where the subscripts L and U indicate estimated values of the parameters at the asymptotes of the rarefaction curves for landscapes including cushion samples and cushion-free areas, respectively (Badano and Cavieres 2006a).

Substrate temperature

Four cushions ca. 30 cm in diameter, the most abundant size at this elevation (Yang et al. 2010), samples of each species were randomly selected and used throughout the study. A point at least 3 m distant in a random direction from each selected cushion was also chosen. A temperature probe 3.0 mm in diameter and with an active tip length of 5 mm (Center Technology Corp, Taiwan, China) was inserted to a depth of 2 cm in the centre of each cushion, and a second probe was inserted to a similar depth at the selected location in a cushion-free area (Cavieres et al. 2007, 2008). The probes were calibrated in ice-water before use in order to confirm stability and accuracy (deviation from zero <1.0 °C, usually <0.7 °C). All probes were connected to four-channel thermocouple data loggers (Center 309, Center Technology Corporation), programmed to record the temperature every 150 seconds throughout the measurement period. The differences between temperatures within and outside the cushions were analysed using a two-sample t -test.

Soil nutrient concentrations

Soil samples (ca. 500 g, 30 cm in diameter) were collected on 14 August 2009 at a depth of 15 cm from beneath five randomly selected plants of each cushion species, and also from outside the cushions at five randomly selected positions. Samples were placed in fabric bags and stored at 5 °C. The samples were sent to the Soil Analysis laboratory of the Agricultural Institute of Yunnan (<http://www.yaas.org.cn>, Kunming, Yunnan, China) and were analysed within the succeeding 10 days for available nitrogen, phosphorus and potassium. The nutrient concentration data were not normally distributed, so differences in nutrient contents between soil under and outside the cushions were evaluated using a Mann–Whitney non-parametric test. All statistical analyses were conducted by SPSS package, version 16.0 (Chicago, IL, USA).

Results

Differences between plant assemblages in cushions and cushion-free areas

A total of 41 species were recorded, of which 15 were found only within cushions (*P. articulata* and/or *A. polytrichoides*) and five only in cushion-free areas. Six species were only recorded within *P. articulata* and four in *A. polytrichoides* cushions (Table 1).

Rarefaction curves for the habitats created by the two cushion species and for cushion-free areas all reached asymptotes (Figure 3), indicating that the sampling procedure was adequate to fully capture the composition of species assemblages in both cushion and surrounding cushion-free areas. Comparison of species richness in the maximum number of samples indicated that this was higher within cushions than in cushion-free areas on the patch scale. However, the magnitude of these positive effects varied between the two cushion species, and *P. articulata* showed higher species richness than *A. polytrichoides* (Figure 3).

Community level effects of the cushion species on species richness, diversity and evenness

As shown in Figure 4, species richness (S) and diversity (H') at the asymptote of the rarefaction curves were significantly higher for the entire habitat, containing both *P. articulata* and *A. polytrichoides* (S , $P < 0.01$; H' , $P < 0.01$), containing only *P. articulata* (S , $P < 0.01$; H' , $P < 0.01$), or containing only *A. polytrichoides* (S , $P < 0.01$; H' , $P < 0.01$), than in cushion-free areas. The relative increases in species richness due to the presence of *P. articulata*, *A. polytrichoides* and both *P. articulata* and *A. polytrichoides* cushions together were 20%, 13% and 25%, respectively, while increases in absolute species diversity were 6%, 5% and 6%, respectively. Values of S at the asymptote of the rarefaction curves were significantly higher for habitats containing only *P. articulata* cushions than for those containing only *A. polytrichoides* cushions ($P = 0.007$), but the corresponding estimates for H' did not differ significantly ($P = 0.326$; see also Figure 4 (a) and (b)). Values of species evenness were similar for cushion-free areas and the communities containing cushions of either *P. articulata* or *A. polytrichoides* (Figure 4(c)).

Substrate temperature

The temperatures within the *P. articulata* cushions were lower than those in the soil outside the cushions during all the sampling periods (early: $t = -112.9$, $P < 0.01$; middle: $t = -127.9$, $P < 0.01$; late: $t = -56.5$, $P < 0.01$; Figure 5(a)–(c)). Similarly, in the early and late growing seasons, temperatures within the *A. polytrichoides* cushions were significantly lower than those in the soil outside the cushions (early: $t = -38.7$, $P < 0.01$; late: $t = -22.4$, $P < 0.01$; Figure 5(d) and (f)). In the middle period, temperatures

Table 1. Frequency of species within cushions of *Potentilla articulata* and *Arenaria polytrichoides* and in cushion-free areas, at an elevation of 4700 m in the Sino-Himalayas. Endemism indicates that species are distributed only in the Hengduan mountain areas, based on information from *Flora of China* (Wu et al. 1994–2012).

No.	Species	Endemism	Within		Bare ground
			<i>P. articulata</i>	<i>A. polytrichoides</i>	
1	<i>Ajania khartensis</i>	No	0	0	70
2	<i>Anaphalis nepalensis</i>	No	5	20	23
3	<i>Arenaria barbata</i>	No	255	51	47
4	<i>Arenaria trichophora</i>	No	43	0	4
5	<i>Bergenia purpurascens</i>	No	0	27	0
6	<i>Carex atrata</i>	No	425	241	0
7	<i>Carex yulungshanensis</i>	Yes	0	27	0
8	<i>Chamaesium viridiflorum</i>	No	0	32	0
9	<i>Chrysosplenium griffithii</i>	No	27	0	2
10	<i>Corydalis adrienii</i>	Yes	12	0	42
11	<i>Cremanthodium humile</i>	No	0	0	24
12	<i>Draba alpina</i>	No	1	0	130
13	<i>Eriophyton wallichii</i>	No	0	0	3
14	<i>Festuca coelestis</i>	No	62	6	11
15	<i>Festuca rubra</i>	No	22	17	37
16	<i>Gentiana atunsiensis</i>	Yes	4	0	0
17	<i>Juncus leucomelas</i>	No	133	1	1
18	<i>Meconopsis horridula</i>	No	6	0	0
19	<i>Meconopsis integrifolia</i>	No	13	4	12
20	<i>Pedicularis roylei</i>	No	24	3	0
21	<i>Pleurospermum nanum</i>	Yes	84	45	50
22	<i>Pleurospermum amabile</i>	No	10	3	23
23	<i>Polygonum macrophyllum</i>	No	222	45	17
24	<i>Polygonum viviparum</i>	No	82	47	0
25	<i>Potentilla hypargyrea</i>	Yes	11	74	13
26	<i>Primula sinopurpurea</i>	Yes	3	0	0
27	<i>Rheum delavayi</i>	No	6	0	0
28	<i>Rhododendron tapetiforme</i>	No	0	4	0
29	<i>Roegneria tschimganica</i>	No	10	14	1
30	<i>Saussurea pachyneura</i>	No	0	51	1
31	<i>Saussurea quercifolia</i>	No	0	0	21
32	<i>Saussurea velutina</i>	No	58	0	0
33	<i>Saussurea werneroides</i>	No	54	296	0
34	<i>Saxifraga aristulata</i>	No	296	38	39
35	<i>Saxifraga flagellaris</i>	No	1	0	82
36	<i>Saxifraga melanocentra</i>	No	6	8	1
37	<i>Saxifraga moorcroftiana</i>	No	78	23	0
38	<i>Saxifraga wardii</i>	Yes	41	20	9
39	<i>Silene yetii</i>	No	8	0	13
40	<i>Solms-Laubachia linearifolia</i>	Yes	6	0	0
41	<i>Solms-Laubachia xerophyta</i>	Yes	0	0	12

within the cushions of *A. polytrichoides* and in open areas differed little in absolute terms but were still significantly different ($t = 10.0$, $P < 0.01$; Figure 5(e)). The temperature recorded in the open areas never rose above 30 °C.

Soil nutrients

Soil beneath both *P. articulata* and *A. polytrichoides* cushions contained significantly more nitrogen (*P. articulata*: $Z = 2.611$, $P = 0.009$; *A. polytrichoides*: $Z = 2.611$, $P = 0.009$, respectively) and potassium (*P. articulata*: $Z = 2.611$, $P = 0.009$; *A. polytrichoides*: $Z = 2.611$, $P = 0.009$, respectively) than outside the cushions (Table 2). The level of available phosphorus was significantly higher under the *P. articulata* cushions ($Z = 2.611$,

$P = 0.009$), but significantly lower under the *A. polytrichoides* cushions ($Z = -2.095$, $P = 0.036$), than outside the cushions (Table 2). Concentrations of phosphorus and potassium were significantly higher beneath *P. articulata* cushions than beneath *A. polytrichoides* cushions (phosphorus: $Z = 2.611$, $P = 0.009$; potassium: $Z = 2.619$, $P = 0.009$) (Table 2). However, no significant differences in soil nitrogen were found under the cushions of the two species ($Z = -1.358$, $P = 0.175$; Table 2).

Discussion

We found that cushions of *P. articulata* and *A. polytrichoides* from alpine scree contained more species than in the cushion-free areas. Species occurring only in the

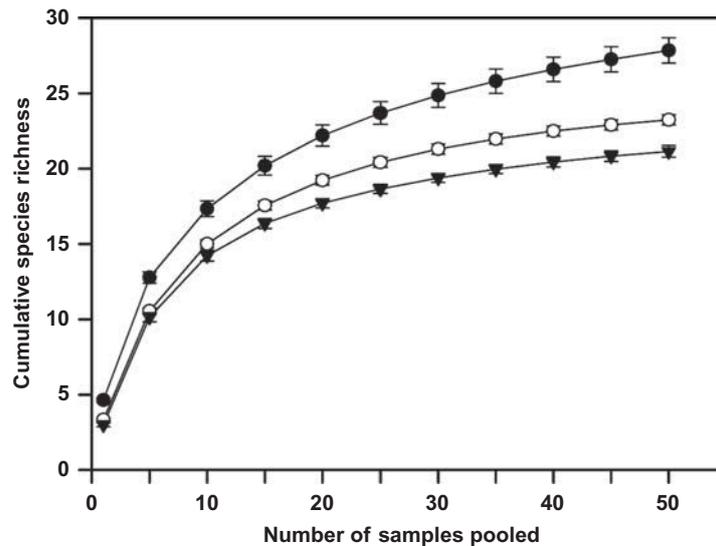


Figure 3. Cumulative species richness estimated from rarefaction curves for each sampling size (\pm 95% confidence intervals) for *Potentilla articulata* cushions (black circles), *Arenaria polytrichoides* cushions (empty circles) and areas outside the cushions (black triangles), at 4700 m elevation in the Sino-Himalayas.

cushions accounted for nearly 40% of the species recorded at the study site. Thus, *P. articulata* and *A. polytrichoides* cushions appeared to provide sufficient microhabitats to increase the species richness and diversity of the plant community substantially at high elevations in the Himalayas. However, our results also indicated that the magnitude of positive association of the two cushion species studied and other plant species differed, with more pronounced effects in enhancing species richness associated with *P. articulata* than *A. polytrichoides* cushions.

Previous studies have found evidence that cushions provide warmer habitats than surrounding open areas on sub-Antarctic mountains (Arroyo et al. 2003; Körner 2003). At our study site, however, cushions of *P. articulata* and *A. polytrichoides* maintained similar or even lower temperatures than open areas. A similar situation was reported in the same region by Yang et al. (2010) and by Dvorský et al. (2013) in alpine habitats of the Trans-Himalayas. These effects may be partly caused by low irradiance due to overcast skies during the summer monsoon of the south-eastern Himalayas. Mitigation of the effect of low temperatures may therefore not have an important microclimatic effect on either of these cushion species. In addition, cushions at low elevations in subtropical mountain areas create microhabitats with a lower frequency of extremely high temperatures in comparison with soil outside the cushions, where temperatures often reaching 35–40 °C (Cavieres et al. 2006, 2008) are not suitable for the establishment and survival of a number of species in the harsh alpine environment (Körner 2003). At our site the recorded temperatures never exceeded 30 °C (see also Yang et al. 2010).

In accordance with previous observations of the effect of cushion plants in the central Chilean Andes and Himalayas (Cavieres et al. 2006, 2008; Yang et al.

2010), the soil beneath the *P. articulata* and *A. polytrichoides* cushions contained higher concentrations of nitrogen and potassium than in the cushion-free areas. In addition, the soil underneath the *P. articulata* cushions contained a higher concentration of phosphorus than in the cushion-free areas. The impact of soil fertility on community structure and diversity is important, particularly in nutrient-poor environments such as desert, alpine and arctic habitats (e.g. West and Klemmenson 1978; Tilman 1987; Theodose and Bowman 1997). In alpine habitats, for example, Theodose and Bowman (1997) found that fertilization led to an increase in plant diversity in a resource-poor dry meadow in the Rocky Mountains, USA. These findings are not surprising, since nitrogen and phosphorus are the nutrients that most commonly limit plant growth in alpine communities (Nagy and Proctor 1997; Körner 2003). Although its effects have been much less intensively studied than those of nitrogen and phosphorus, increases in potassium levels have been found to increase plant resistance to drought and enhance the efficiency of water use (e.g. Bradbury and Malcolm 1977; van den Driessche 1991; Egilla et al. 2001). The role of potassium in nutrient-poor environments has also recently been identified as being important in facilitation (Gómez-Aparicio et al. 2005; Cavieres et al. 2008; Yang et al. 2010). In terms of cushion plants, Yang et al. (2010) related the greater facilitation of *A. polytrichoides* cushions at increasing elevations in the south-eastern Himalayan region to lower soil potassium content at higher elevation. At our site the two cushion plants could therefore produce “fertilized islands” for other plant species.

Our results showed that the enhancement of species richness by *P. articulata* cushions was greater than that for *A. polytrichoides* cushions. Similar differences in the nurse

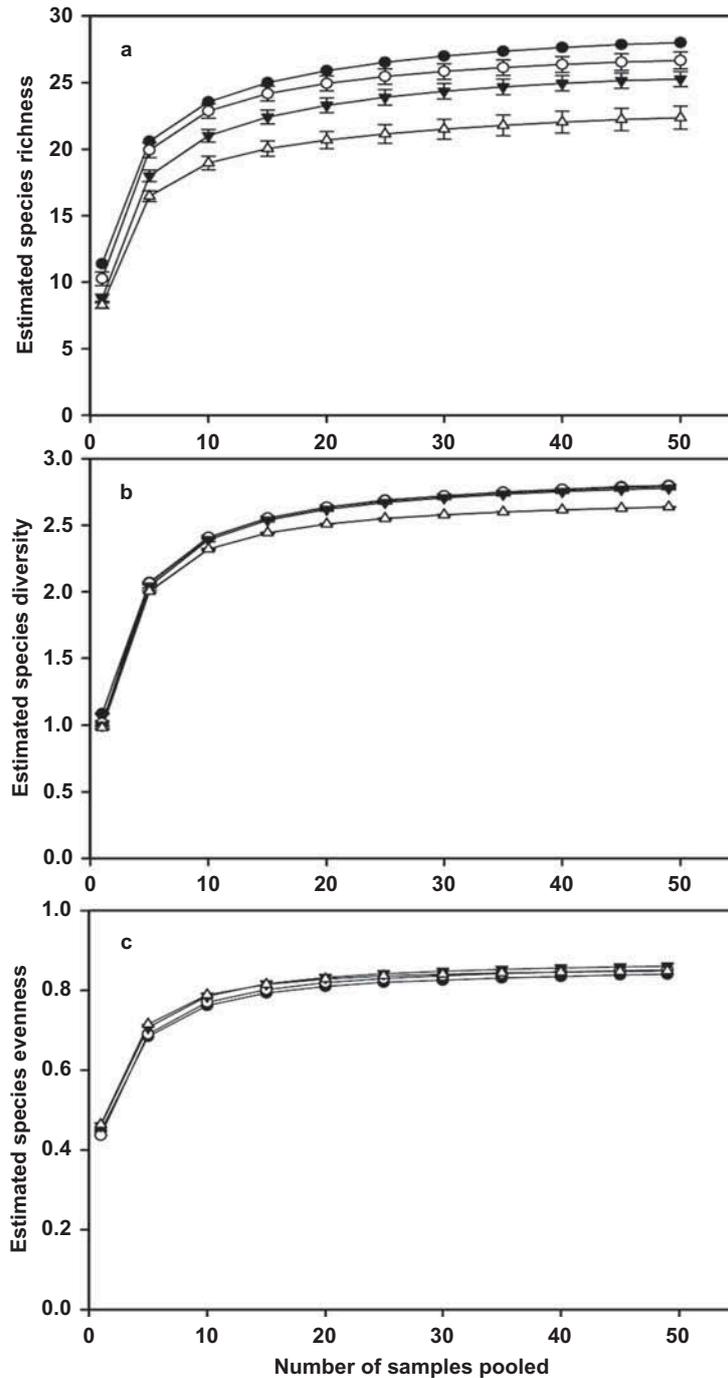


Figure 4. Estimated values (\pm 95% confidence intervals) of (a) species richness, (b) species diversity, and (c) species evenness, for communities including *Potentilla articulata* cushions (empty circles), *Arenaria polytrichoides* cushions (black triangles), both *P. articulata* and *A. polytrichoides* cushions (black circles) and areas outside the cushions (empty triangles), at 4700 m elevation in the Sino-Himalayas.

effect of cushion plants were observed by Cavieres and Badano (2009) in the high Andes. It has been suggested that the effect of nurse species on other species is dependent on the extent to which resources and stresses are altered in particular environments (Holmgren et al. 1997; Callaway 2007). In the high Andes these differences are related to differences in the amelioration of high temperatures and potassium content within cushion structures

(Cavieres et al. 2006). In our study, although both the species examined enhanced nitrogen levels to a similar degree, soil samples collected beneath *P. articulata* cushions had roughly three- and four-fold higher concentrations of potassium and phosphorus, respectively, than soil samples collected beneath *A. polytrichoides* cushions. These differences in nutrients were probably due to species-specific effects of the plants on nutrient cycling

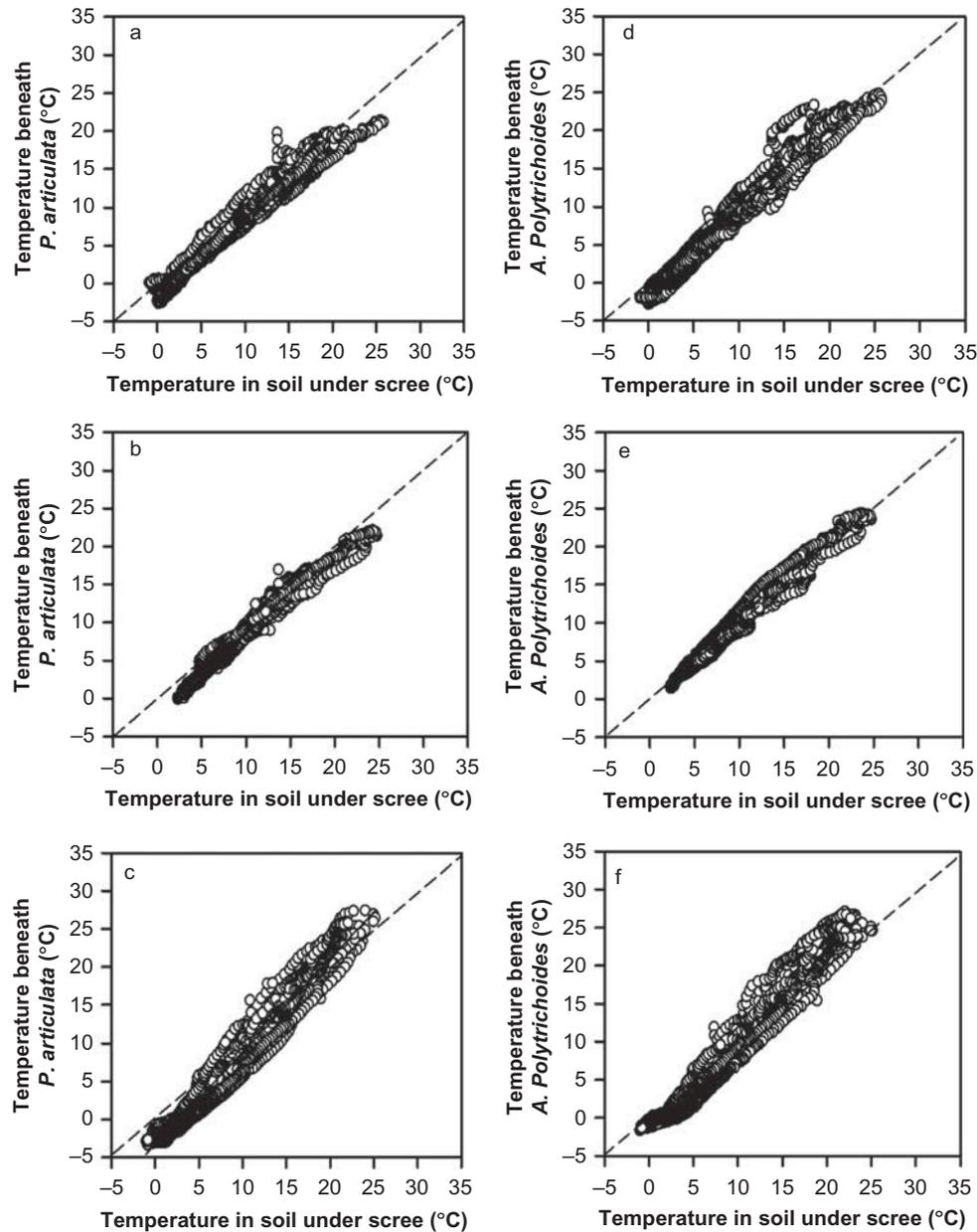


Figure 5. Temperatures recorded during the early (a, d), middle (b, e) and late (c, f) sampling periods of the growing season within *Potentilla articulata* cushions and in the soil under scree (a–c), and within *Arenaria polytrichoides* cushions and in the soil under scree (d–f) at 4700 m elevation in the Sino-Himalayas.

Table 2. Available nitrogen (N), phosphorus (P) and potassium (K) concentrations (mg/kg) in soils below cushions of *Potentilla articulata*, *Arenaria polytrichoides* and in cushion-free areas at the study site (4700 m elevation in the Sino-Himalayas).

Microhabitat	N	P	K
<i>Potentilla articulata</i>	259.72 (\pm 34.71)	8.55 (\pm 1.64)	625.6 (\pm 122.07)
<i>Arenaria polytrichoides</i>	189.06 (\pm 14.96)	2.53 (\pm 0.58)*	236.34 (\pm 7.33)*
Bare ground	52.15 (\pm 4.54)*	4.24 (\pm 0.46)*	99.64 (\pm 4.84)*

Note: Data are mean values (\pm s.e). Asterisks indicate significant differences ($P < 0.05$).

(Hobbie 1992). Given that the effect of our cushion species on soil temperature and nitrogen content did not differ significantly, the variation in their effect on species richness may be related to differences in the phosphorus and potassium levels in the soil beneath them.

In contrast with the studies of de Bello et al. (2011) and Dvorský et al. (2013), which showed that cushion plants did not act as facilitators at extremely high, cold and dry locations in the north-western Himalayas and the Trans-Himalayas, our results combined with findings

presented by Yang et al. (2010) demonstrate the importance of the facilitation by cushion plants of the structuring of plant communities at high elevations in the south-eastern Himalayas. It has long been suggested that the importance of positive interactions between species may be greater as the environment becomes more stressful (reviewed by Holmgren and Scheffer 2010). However, Michalet et al. (2006) suggested that the importance of positive interactions could decrease or diminish at both extremes of a stress gradient, where the species present may be stress tolerant and would not necessarily profit from facilitation. The site examined by de Bello et al. (2011) in the north-western Himalayas was located at a higher elevation (5900 m, ca. 1200 m higher than our site), that was not affected by the summer monsoon (with precipitation of 100 mm year⁻¹, ca. 600–700 mm less annual precipitation than at our site). At the extremely cold and dry region of the Trans-Himalayas, Dvorský et al. (2013) found that *Thylacospermum caespitosum* cushions did not ameliorate the microclimatic factors such as temperature, water content and soil nutrients within their cushions, and they could therefore compete with other species. In the central Chilean Andes, the reduced effect of cushions under drier conditions have also been reported (Cavieres and Badano 2009). Therefore, the apparently contradictory results relating to the interaction between cushion plants and other plant species in the Himalayas probably reflect differences in temperature and water conditions in the different regions.

It is well known that other factors, such as the evolutionary relationship (e.g. Butterfield et al. 2013), differences in functional traits (Michalet et al. 2011; Schöb et al. 2012, 2013a) or indirect interactions (Schöb et al. 2013b) between the nurse cushion species and the beneficiary species, also play an important role in the outcome of plant–plant interactions in alpine habitats in general, and in cushion-dominated communities in particular. In order to more fully understand the positive or negative association of cushion species among other non-cushion species at high elevations in the Himalayas, further studies are therefore needed, combining different characteristics of benefactor and beneficiary species.

On the broader scale, cushions of *P. articulata* and *A. polytrichoides* at our study site appeared to have weaker effects on species richness and diversity (increasing these variables by ca. 10–20% and 5–6%, respectively) than cushion species in the high Andes (ca. 20–240% and 20–110%, respectively; Badano and Cavieres 2006a). In addition, our results indicate that species evenness does not differ significantly between cushion-free areas and patches modified by *P. articulata* or *A. polytrichoides* cushions. Cavieres and Badano (2009) suggested that, in addition to the mitigation of adverse environmental conditions, the species-specific effects of cushion plants on species richness may reflect the intensity of abiotic stress experienced by plants in microhabitats away from the cushions. Large variations in surface temperature, accompanied by scarce rainfall during the summer, characterise the Mediterranean

regions of the high Andes (Cavieres et al. 2006, 2007, 2008). In terms of temperature, Cavieres et al. (2007) reported that soil temperatures in the bare ground of the alpine zone in the central Andes dropped to 0 °C or below on ca. 30% of days during the growing season, whereas daytime temperatures frequently reached 35–40 °C (see also Cavieres et al. 2008). Moreover, an extended summer drought of 5–6 months is not uncommon in these parts of the Andes (Mooney and Dunn 1970). Further, Cavieres et al. (2006, 2008) reported that the average available nitrogen content in open areas at high elevations in central Chile was ca. 1 mg kg⁻¹; much lower than the concentrations in the soil samples recorded at our study site. However, mountain areas in the south-eastern Himalayas seldom experience such stressful environmental conditions, probably due to the summer monsoon climate. These differences in climate and soil nutrition may explain the differences observed between the habitat engineering of plants with cushion growth forms in the Himalayas and the Andes.

Conclusions

Our study provides new evidence that facilitation by cushion plants can be a key factor in enhancing the species richness and diversity of plant communities in high-elevation habitats. Such changes are probably related to increases in soil nutrient concentration associated with the cushions, which should promote the establishment and growth of individual plants and will ultimately change the structure of the plant community. Further, our results indicate that this effect varies and is benefactor-dependent, probably due to differences in nutrient concentrations under different cushion species.

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Appendix

Daytime (08:00–20:00h) data for mean (\pm SE), maximum and minimum air temperature (T_a , °C), solar radiation (I , $\mu\text{mol}^{-1} \text{m}^{-2} \text{s}^{-2}$), relative humidity (RH, %) above ground level during the early, middle and late periods of the growing season in 2009. Means presented in the table are for 12 h of values recorded every 5 min during the sampling periods. Weather conditions during the measuring periods included: four sunny days and three rainy days with some snow in the early period; six rainy days and one cloudy day with some rain in the middle period; five sunny days and two cloudy days during the late growing season.

	Early period			Middle period			Late period		
	T_a	I	RH	T_a	I	RH	T_a	I	RH
Mean (SE)	7.73 0.15	701.38 19.93	71.75 0.75	7.52 0.96	507.78 13.30	88.96 0.32	6.92 0.16	653.04 21.39	69.94 0.64
Maximum	19.04	2637.00	97.00	18.04	2081.00	97.90	19.05	2627.40	97.90
Minimum	0.84	13.64	24.00	1.99	2.88	51.65	−0.98	0	29.93