



# Cushion plants can have a positive effect on diversity at high elevations in the Himalayan Hengduan Mountains

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## Keywords

Alpine habitats; Cushion plants; Environmental severity; Facilitative interactions; Himalayan Hengduan Mountains; Nurse trait effects; Species richness

## Nomenclature

The International Plant Name Index (IPNI) ([www.ipni.org](http://www.ipni.org); accessed on 20 May 2014)

Received 4 August 2014

Accepted 2 January 2015

Co-ordinating Editor: Richard Michalet

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## Introduction

Mountain systems support approximately one-third of terrestrial plant diversity (Barthlott et al. 1996). Within

## Abstract

**Questions:** What is the community-level consequence of biotic processes, in particular the importance of facilitation, in determining patterns of diversity in alpine plant communities of the Himalayan Hengduan Mountains? Does facilitation intensity change with environmental severity, and are these changes due to environmental severity or nurse trait effects?

**Location:** Eleven alpine plant communities dominated by cushion plants in the Himalayan Hengduan Mountains, within the mountain system of south-central China.

**Methods:** We determined plant species richness and abundance in habitats created by cushions and cushion-free areas, and assessed the cushion effects on species richness and abundance with rarefaction curves and the relative interaction index, respectively. We examined the relationship between cushion effects on diversity and habitat severity and tested if changes in the net cushion effects along the severity gradient were due to a change in the performance of species without cushions (environmental severity effect) and/or with cushions (nurse trait-mediated effect).

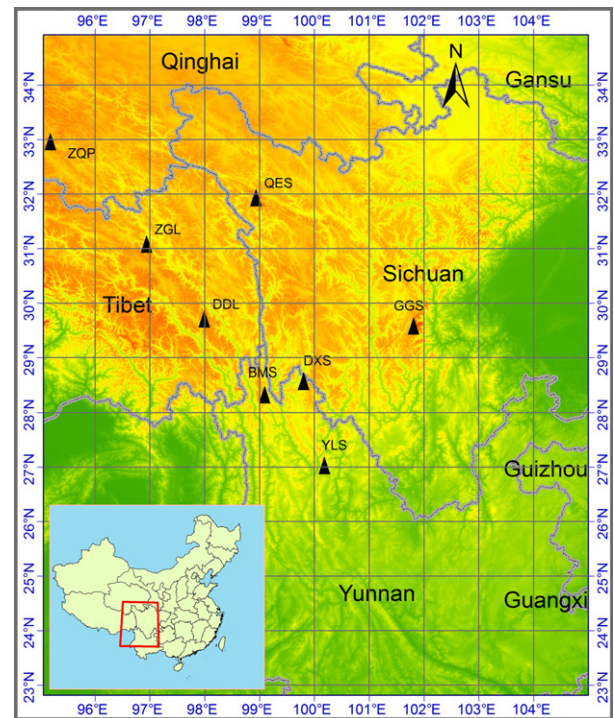
**Results:** The presence of cushion plants increased species richness and abundance in most studied plant communities. The net facilitation effect of cushions increased with increasing habitat severity, an effect that could be attributed mainly to a reduction in species richness in cushion-free areas with increasing severity. However, the changes in magnitude of facilitation of particular cushion species growing in high and low severity habitats could be attributed to both environmental severity and neighbour trait effects. Despite the overall positive effect of cushion plants on plant species richness, not all cushion species contributed to higher species richness. The deviation of individual cushion species from the general pattern of increasing facilitation with increasing severity indicated the species specificity of facilitation depends on the traits of nurse species.

**Conclusion:** The presence of cushion plants generally increased species richness in alpine plant communities of the Himalayan Hengduan Mountains, with the importance of the cushion effect increasing with habitat severity due to a buffering effect by cushions of the negative effect of habitat severity on species richness observed in cushion-free areas. This indicates the pivotal role of facilitative interactions among plant species in supporting high diversity in these severe environments.

mountain regions, the alpine zone, located above the climatic tree line and below the permanent snow line, supports around 8000–10 000 higher plant species, accounting for ca. 4% of all known higher plant species

(Körner 2003). Results from comparison of ten different Asiatic mountains and the European Alps indicated that the alpine flora seems to represent about one-fifth to one quarter of the total regional flora, including that found on the plateau of those regions (Agakhanjanz & Breckle 1995; Körner 2003). Indeed, many alpine regions are considered to be biodiversity hotspots. The high degree of plant diversity in mountain areas has mainly been attributed to abiotic factors, such as geographic isolation, tectonic uplift and strong microhabitat differentiation (Packer 1974; Agakhanjanz & Breckle 1995; Körner 1995). The role of biotic factors (facilitation/competition) in structuring plant communities at high elevations has received some recent attention (reviewed by Anthelme et al. 2014). In a global set of experiments in mountain plant communities, Callaway et al. (2002) drew the general conclusion that while competition commonly dominates interactions at low elevations, interactions between plant species at high elevations, where abiotic stress is high, are predominately facilitative. These facilitative effects have strong influences on the local diversity of plant communities in alpine regions (e.g. Kikvidze et al. 2005; Cavieres & Badano 2009; Butterfield et al. 2013; Cavieres et al. 2014). Such positive effects of facilitating species through their effects on the local environment may also be relevant for the impact of on-going environmental changes, such as climate change, on biodiversity. Facilitating species may provide efficient biotic refuges for up-migrating plants during primary succession of newly available areas (Anthelme et al. 2014). Understanding facilitation is, therefore, not only crucial for understanding current biodiversity of alpine plant communities but also for predictions of alpine plant community responses to a changing climate (Anthelme et al. 2014).

The mountains of south-central China are one of the most biologically rich temperate regions on Earth (Sherman et al. 2008). Within this unique area, the Himalayan Hengduan Mountains (HHM, 24°40'–34°00' N, 96°20'–104°30' E; Li 1987; Fig. 1), oriented north–south along the eastern flanks of the Himalayas and southeast of the Qinghai Tibetan Plateau, have been identified as a hotspot for temperate biodiversity (Mittermeier et al. 1999), supporting the globally richest alpine flora (Xu et al. 2014a). It is reported that the alpine subnival belt (ca. 4300–5200 m a.s.l.) between the upper alpine belt and the nival belt in HHM harbours over 900 true alpine species (Xu et al. 2014a). In addition, a quantitative assessment of the alpine flora across areas in the southeast HHM indicated an average of 59 species per 60 m<sup>2</sup> (Sherman et al. 2008). The high degree of plant diversity in this region is related to its location at a biogeographical convergence zone of temperate and tropical areas and its monsoonal climate (reviewed in Xu et al. 2014b). However, to our knowledge, the role



**Fig. 1.** Map showing the study region of the Himalayan-Hengduan Mountains and the 11 study sites. From north to south: ZQP: Zhaqing snow mountain. Dominant cushion species: *Sibbaldia tetrandra* [ZQP (SB)]; QES: Queer snow mountain. Dominant cushion species: *Arenaria polytrichoides* [QES (AP)] and *Chionocharis hookeri* [QES (CH)]; ZGL: Zhuogela snow mountain. Dominant cushion species: *Thylacospermum caespitosum* [ZGL (TC)]; DDL: Dongdala snow mountain. Dominant cushion species: *A. lancangensis* [DDL (AL)] and *Arenaria densissima* [DDL (AD)]; GGS: Gongga snow mountain. Dominant cushion species: *Potentilla articulata* [GGS (PA)]; DXS: Daxue snow mountain. Dominant cushion species: *Arenaria lancangensis* [DXS (AL)]; BMS: Baima snow mountain. Dominant cushion species: *Potentilla articulata* [BMS (PA)] and *Arenaria polytrichoides* [QES (AP)]; YLS: Yulong snow mountain. Dominant cushion species: *Arenaria oreophila* [YLS (AO)].

of biotic processes, particularly facilitation, in structuring patterns of plant community diversity at high elevations in the HHM remains unclear.

One prominent example of facilitative interactions among plant species involves organisms referred to as 'nurse species' (also called 'engineering species'; Jones et al. 1994, 1997), which alter the distribution of material and energy in the abiotic environment through non-trophic and trophic interactions, thus creating and maintaining new habitat patches in the landscape (Jones et al. 1994, 1997; Molenda et al. 2012). Within high-alpine regions, species that have a cushion morphology often act as 'nurses' due to their ability to moderate environmental conditions with respect to temperature, water and soil nutrition (e.g. Molina-Montenegro et al. 2006; Cavieres et al. 2007, 2008; Yang et al. 2010). Such species, there-

fore, play an important role in structuring alpine plant communities at both regional (e.g. high Andes, Badano & Cavieres 2006a,b; Cavieres & Badano 2009) and global scales (Butterfield et al. 2013; Cavieres et al. 2014). Cushion plants also occur in the alpine belt of the HHM, where previous single-site studies showed positive effects of cushion species on other plant species (Yang et al. 2010; Chen et al. 2014). However, in order to understand the context dependence of this facilitative effect of cushions on species diversity in the HHM, a large-scale sampling to assess the effects of cushion plants on plant diversity is needed. This would reveal the relative importance of facilitation for species diversity across environmental gradients in the HHM and allow estimating the relevance of nurse species for biodiversity under climate change scenarios.

A recent meta-analysis using data from 16 alpine experiments across different regions showed that the global pattern of shift from competition to facilitation with increasing altitude can be due to a change in the performance of species without nurses (i.e. environmental severity effect) and/or with nurses (i.e. nurse traits effect; Michalet et al. 2014). However, such attempts to separate nurse trait effects from environmental severity effects along stress gradients are very rare in nurse plant studies (but see Schöb et al. 2013), but relevant to assess the importance of facilitation under future climatic conditions (Michalet et al. 2014). To gain a broad understanding of facilitation by cushion plants and their impact on community-level species diversity in alpine communities in the HHM, we selected 11 alpine plant communities dominated by cushion species and located in different areas (Fig. 1) to examine: (1) whether cushion plants have positive effects on local diversity (i.e. increasing species richness and abundance) at the upper altitudinal limit for alpine plants in the HHM; and (2) whether there is a relationship between the facilitative effect of cushion species at the community level and environmental severity. Additionally, we also specifically ask (3) if changes in the effect size of cushion species on species diversity along severity gradients are due to environmental severity and/or nurse trait effects.

## Methods

### Study areas and target cushion species

The climatic pattern of the HHM is monsoonal, with wet summers and dry winters. There is a general trend of decreasing annual mean temperature from south to north, with values from 0 to >20 °C, and minimum and maximum values generally occurring in January and July, respectively (Zhang et al. 1997). Similar to temperature, annual precipitation tends to decrease from south to north, with values between 300 and 1300 mm, mostly concen-

trated during the summer (early Jun–late Sept; Zhang et al. 1997). In this region, alpine meadows commonly occur at 4000–4500 m a.s.l, with scree slopes at higher elevations. Permanent snow and ice occur at ca. 5200 m.

A total of 11 alpine plant communities dominated by cushion species, at eight different sites, were selected (Fig. 1). From north to south, we sampled *Sibbaldia tetrandra* at Zhaqing Snow Mountain Pass in northern HHM; both *Chionocharis hookeri* and *Arenaria polytrichoides* at Queer Snow Mountain Pass in western HHM; *Thylacospermum caespitosum* at Zhuogela Snow Mountain in northeastern HHM; both *A. lancangensis* and *A. densissima* at Dongdala Snow Mountain in central HHM; *Potentilla articulata* at Gongga Snow Mountain in southwestern HHM; *A. lancangensis* at Daxue Snow Mountain in southeastern HHM; both *P. articulata* and *A. polytrichoides* at Baima Snow Mountain in southeastern HHM; and *A. oreophila* at Yulong Snow Mountain in southern HHM. All 11 communities are in early successional stages and characterized by open plant communities with patchy vegetation (Li et al. 1981). The selected target species dominated the selected plant communities in the study region. Although very little is known about the growth rate of each studied cushion species, it has been suggested that large cushions may have taken decades or even longer to reach their present size, and may yet continue to live for a long period of time due to their high rates of survival (Morris & Doak 1998; Kleier & Rundel 2004).

As a highly stress-tolerant species, cushions often dominate the upper limit of alpine vegetation, particularly on bare soils, windswept habitats or glaciated margins characterized by poor nutrient availability and cool environments (Körner 2003). Assuming an upward migration of plants into higher elevations due to the effects of global warming (Baker & Moseley 2007) and potential relevance of facilitation by cushion plants for this shift (Anthelme et al. 2014), the sampling sites were chosen to be located as close as possible to the upper altitudinal limit of the cushion distributions. This allowed us to examine the facilitative effect of the cushion plants on other plant species at the leading edge of the expected migration process. By choosing the upper altitudinal limits of the cushion plants as study sites we also avoided rangeland and therefore minimized possible disturbances from human-related activities (e.g. pasturing) in this otherwise heavily pastured region of the Qinghai-Tibetan Plateau (Miehe et al. 2011; Haynes et al. 2013; see App. S1 for detailed information on study sites and sampling intensities).

### Sampling of species in cushions and cushion-free areas

At each study site, we randomly selected individual cushions (with no senescent or damaged parts) and followed

the protocol of Cavieres et al. (2014) for the plant diversity sampling. All plants growing within the selected cushions were identified to species level, and the number of individuals of each species was counted. Since cushions are usually elliptical, we also measured the longest and shortest axes of each cushion in order to estimate its area. To obtain comparable samples of species in surrounding open areas, the shape of each sampled cushion was replicated using a wire ring. These rings were randomly placed in open areas at least 1 m away from cushions, then all plant individuals within the wire rings were identified to species level, and the number of individuals counted. In addition, we collected all of the aerial parts of species within the cushion patches and in the equivalent sampled open areas. All samples were stored in paper bags (one bag per plot). The bags were then placed in a drying oven at 75 °C for 40 h before being weighed to determine the above-ground total dry biomass of plants within each sample. The biomass data in cushion-free areas at each study site were averaged and used as an indicator of environmental severity (see below).

#### Comparison of species richness and species abundance between cushions and cushion-free areas

To compare species richness of different habitat types (i.e. cushion and cushion-free areas), we generated a species  $\times$  samples matrix for each habitat type in each site, where each cell ( $i, j$ ) contained the abundance of the  $i$ th species in the  $j$ th sample; we used this to determine the effect of cushion plants on species richness within and outside cushions in each of the 11 communities. From the matrices, 500 samples were randomly drawn, with replacement, for each sample size (from one sample to the maximum number of samples); then the species richness of the 500 samples was calculated using Coleman's algorithm (Coleman et al. 1982). To avoid bias due to differences in the samples that were replaced, we ran the rarefaction analysis for cushion and cushion-free areas at each site 20 times. Maximum likelihood estimates of species richness for cushions and cushion-free areas at the asymptote of the sample-based rarefaction curves were averaged and plotted. The rarefaction analyses were carried out with EstimateS v. 9.01 software (Colwell 2000, University of Connecticut Storrs, CT, USA). The increase in species richness for each studied community due to the presence of a cushion species (ISR) was calculated as  $ISR = [(S_C - S_O)/S_O] \times 100\%$ , where  $S_C$  and  $S_O$  are estimated values for species richness in cushion and open (cushion-free areas) plots, respectively, at the asymptotes of sample-based rarefaction curves (Cavieres et al. 2014).

In order to examine the impact of cushions on the abundance of non-cushion species, we calculated the relative interaction index ( $RII_{abundance}$ ) for each non-cushion

species in each community (Armas et al. 2004). Following the protocol of Cavieres et al. (2014),  $RII_{abundance} = (\# \text{ within cushion species} - \# \text{ in open area}) / (\# \text{ within cushion species} + \# \text{ in open area})$ , where  $\#$  indicates the number of individuals of each non-cushion species. Thus,  $RII_{abundance} = 1$ , when all individuals of a species occur within cushions;  $RII_{abundance} = 0$ , when all individuals of a species are distributed equally between cushions and open areas; and  $RII_{abundance} = -1$ , when all individuals of a species occur within cushion-free areas. Mean  $RII_{abundance}$  across all species within a community was then used as an estimate for the average effects of the cushion species on other plant species at that site (Cavieres et al. 2014). In addition, the proportion of species unique to cushion habitats and cushion-free areas was also determined in each community.

#### Relationship between habitat severity and effect size of facilitation by cushion species

Habitat severity can be reflected through habitat productivity (biomass per area and unit time,  $g \cdot m^{-2} \cdot yr^{-1}$ ), with the latter shown to be positively related to habitat biomass under stressful conditions (Noy-Meir 1975; Weiner 2001). In order to test whether there is a relationship between habitat biomass and environmental severity in our study, we assessed the relationship of habitat biomass with effective precipitation (EP; de Martonne 1927) during the growing season (Jun, Jul and Aug) of each site. EP has been used previously as a surrogate for environmental stress (Kikvidze et al. 2006; Cavieres & Badano 2009) because it is generally highly correlated with habitat productivity (Stadler 2005). Indeed, habitat biomass was highly correlated with EP in our study ( $r = 0.631$ ,  $P = 0.037$ ; App. S2).

To explore the relationship between habitat severity and the facilitative effects of cushion plants, we examined the correlation between ISR and mean  $RII_{abundance}$  and habitat biomass (above-ground biomass in cushion-free areas,  $g \cdot m^{-2}$ , log transformed) across all studied communities using Spearman's rank correlation implemented in SPSS (SPSS, Chicago, IL, US).

#### Environmental severity effect and nurse trait effect in facilitation of cushion species

The relative effect of the environment and nurse traits on changes in the cushion effect size on species richness along the severity gradient was assessed by calculating  $RII_{environment}$  and  $RII_{neighbours}$ , as suggested in Michalet et al. (2014), for three cushion species inhabiting both high (low severity) and low (high severity) biomass habitats (i.e. *A. polytrichoides*: QES vs BMS; *A. lancangensis*: DDL

vs DXS; *P. articulata*: GGS vs BMS).  $R_{II_{neighbours}} = (\# \text{ with nurse} - \# \text{ without nurse}) / (\# \text{ with nurse} + \# \text{ without nurse})$ ,  $R_{II_{environment}} = (\# \text{ at low biomass habitat} - \# \text{ at high biomass habitat}) / (\# \text{ at low biomass habitat} + \# \text{ at high biomass habitat})$ , where # indicates species richness.  $R_{II_{neighbours}}$  was calculated separately for high and low stress habitats, indicating the effect size of cushions on species richness at high and low severity habitats, respectively, with  $R_{II_{neighbours}}$  below 0 pointing towards competition and above 0 indicating facilitation. In contrast,  $R_{II_{environment}}$  was calculated separately for species growing with and without cushions, indicating the effect size of environmental severity on species richness either when growing with or without a nurse, where  $R_{II_{environment}}$  below 0 indicates higher species richness at the low severity habitat and above 0 indicates higher species richness at the high severity habitat (Michalet et al. 2014). If there is a significant change in  $R_{II_{neighbours}}$  between low and high stress habitats, then  $R_{II_{environment}}$  can be used to attribute the change in the effect size of facilitation along the severity gradient to an environmental severity effect (if  $R_{II_{environment}}$  without cushions is significantly different from 0), to a nurse trait effect (if  $R_{II_{environment}}$  with cushions is significantly different from 0) or to a combined environmental severity and nurse trait effect (if  $R_{II_{environment}}$  with and without cushions are significantly different from 0) (Michalet et al. 2014). The results of each index of the three species were averaged and a paired sample *t*-test in SPSS was used to examine the difference in  $R_{II_{neighbours}}$  between high and low stress habitats and  $R_{II_{environment}}$  between cushion and open habitats, and one sample *t*-tests were used to examine the difference of  $R_{II_{environment}}$  with and without cushions from 0.

## Results

### Cushions generally increased species richness and abundance

There were significant differences in species richness between cushions and cushion-free areas for all studied 11 sites, with ten communities showing significantly higher species richness in cushions than in cushion-free areas (Fig. 2a). Richness within cushions of *A. polytrichoides* at QES differed little from cushion-free areas but was still significantly lower. With the exception of *A. polytrichoides* at QES, the increase in richness associated with the presence of cushions ranged from ca. 5% (*T. caespitosum* at ZGL) to ca. 59% (*A. lancangensis* at DXS). Differences in richness effects for particular species at different sites ranged from ca. 13% in *A. polytrichoides* (QES vs BMS) to ca. 33% in *A. lancangensis* (DDL vs DXS). In addition, species differences in richness effects within a site were observed for *A. polytrichoides* and *P. articulata* in BMS (ca. 31%). Eight

of the 11 communities (73%) significantly increased mean species abundance, i.e. showing positive  $R_{II_{abundance}}$  values (Fig. 2b). There was a marginally significant difference in  $R_{II_{abundance}}$  among different studied communities ( $F = 1.731$ ,  $P = 0.07$ ). The proportion of species unique to cushion habitats ranged from 10% (*A. polytrichoides* at QES) to 40% (*A. lancangensis* at DXS; Table 1).

### Cushion effects tended to increase with habitat severity

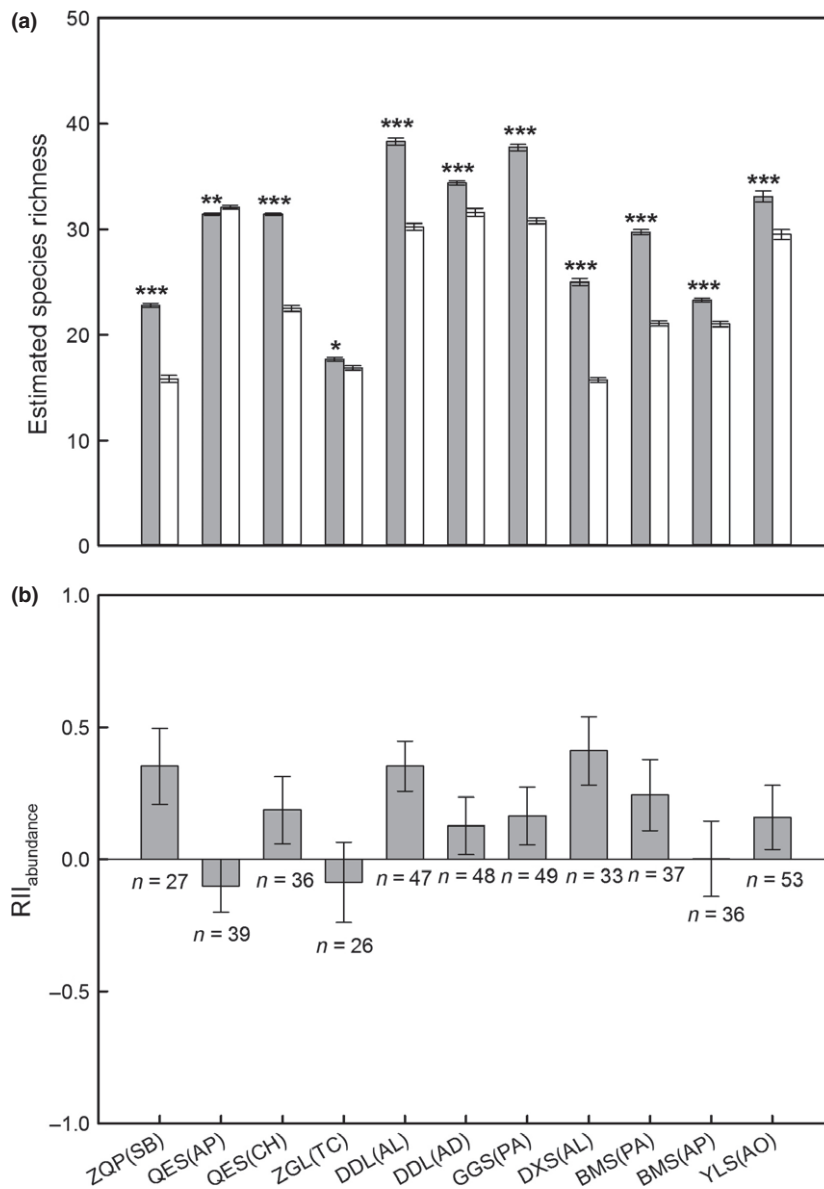
Both ISR ( $n = 11$ ,  $r = -0.55$ ,  $P = 0.07$ ) and  $R_{II_{abundance}}$  ( $n = 11$ ,  $r = -0.56$ ,  $P = 0.07$ ) showed almost significant correlations with habitat biomass, with facilitation intensity decreasing as habitat biomass increased (Fig. 3a,b).

### Changes in facilitation intensity with habitat severity due to environmental severity and nurse trait effects

Mean  $R_{II_{neighbour}}$  showed positive values for low and high severity sites, indicating that there was a significant facilitation effect of the cushions (Fig. 4). Furthermore,  $R_{II_{neighbour}}$  in the high severity habitats was significantly higher than  $R_{II_{neighbour}}$  at low severity habitats ( $n = 3$ ,  $t = -4.722$ ,  $P = 0.042$ ). Negative values (below zero) of  $R_{II_{environment}}$  both with and without cushions indicated higher species richness at the low severity habitat (Fig. 4). In addition, both values of  $R_{II_{environment}}$ , i.e. without ( $n = 3$ ,  $t = -5.791$ ,  $P = 0.029$ ) and with ( $n = 3$ ,  $t = -5.920$ ,  $P = 0.029$ ) cushions, were significantly different from zero, indicating the changes of facilitation of cushions were due to both environmental severity and nurse trait effects. However,  $R_{II_{environment}}$  without neighbours was significantly more negative than with neighbours ( $n = 3$ ,  $t = 4.889$ ,  $P = 0.039$ ), indicating that with increasing environmental severity, species richness in habitats without cushions decreased more strongly than species richness within cushions (Fig. 4). Similar patterns were observed for each species separately (App. S3).

## Discussion

Our results support the hypothesis that facilitation performed by cushion nurse plants acts as an important driving force in enhancing species richness and abundance of alpine plant communities in the Himalayan Hengduan Mountains. This highlights the importance of biotic processes in regulating diversity in these natural plant communities. Similar enhancements of species richness and abundance due to the presence of cushions were reported in many other alpine areas (e.g. Reid et al. 2010; Antelme et al. 2012; Cavieres et al. 2014) but are new to the very species-rich flora of the mountains in south-central China.



**Fig. 2.** (a) The number of species estimated by rarefaction curves (mean  $\pm$  SE) within cushions (gray bars) and cushion-free areas (white bars) in each studied community ( $n = 20$ , the number of replicated rarefaction analyses). \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . (b) Mean relative interaction index (RII<sub>abundance</sub>) (mean  $\pm$  SE) of cushion species in each studied community ( $n =$  number of non-cushion species). See Fig. 1 for abbreviations.

### Environmental context dependence of facilitation

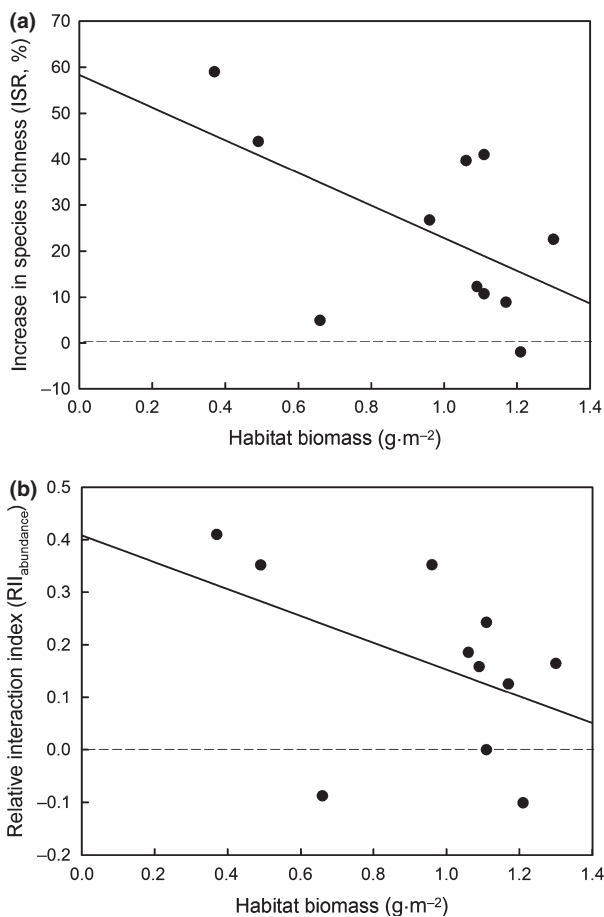
We found an increase of facilitation effects of cushions as habitat severity increased. This provides support for the stress-gradient hypothesis (SGH), which proposes that competition should be relatively more frequent in low-stress conditions and facilitation more frequent in high-stress conditions (Bertness & Callaway 1994; Brooker & Callaghan 1998). Even though habitat biomass, our surrogate of environmental severity, is susceptible to other factors than abiotic environmental harshness, in particular to

herbivory, with the location of the study sites at the upper altitudinal limit of plants we considerably reduced the impact of such potential confounding factors. All our study sites were characterized by open vegetation, suggesting very low grazing intensity (Dorji et al. 2010, 2014).

In addition, our study indicated that the change in facilitation of cushion species was driven by an environmental severity effect (i.e. the richness of non-cushion species in cushion-free areas decreased significantly with increasing severity of the habitat). In fact, richness of non-cushion species also decreased in cushions (shown as a negative

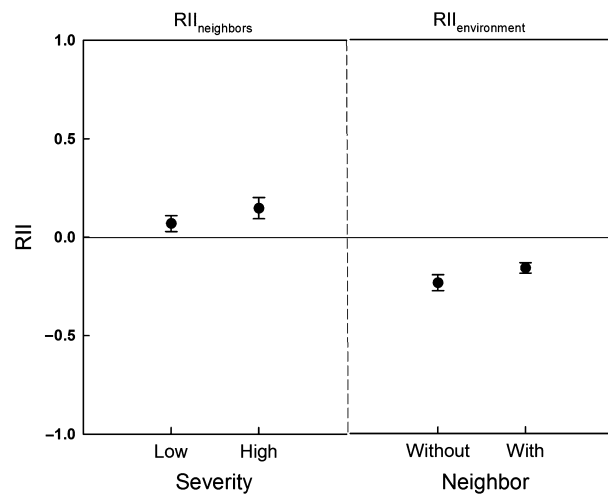
**Table 1.** Total number of species, number of species unique to either cushions or cushion-free areas and number of species found in both cushions and cushion-free areas in each plant community studied in the Himalayan Hengduan Mountains. See Fig. 1 for full names of study sites.

Study sites	Cushion Species	Total Species	Species Unique to Cushions (% Total Species)	Species Unique to Cushion-Free Areas (% Total Species)	Shared Species
ZQP	<i>Sibbaldia tetrandra</i>	27	8 (30)	2 (7)	17
QES	<i>Arenaria polytrichoides</i>	39	4 (10)	7 (18)	28
QES	<i>Chionocharis hookeri</i>	36	10 (28)	7 (19)	19
ZGL	<i>Thylacospermum caespitosum</i>	26	4 (15)	6 (23)	16
DDL	<i>Arenaria lancangensis</i>	47	10 (21)	6 (13)	31
DDL	<i>Arenaria densissima</i>	48	9 (19)	10 (21)	29
GGs	<i>Potentilla articulata</i>	49	14 (29)	7 (14)	28
DXS	<i>Arenaria lancangensis</i>	33	14 (42)	6 (18)	13
BMS	<i>Potentilla articulata</i>	37	11 (30)	6 (16)	20
BMS	<i>Arenaria polytrichoides</i>	36	9 (25)	11 (30)	16
YLS	<i>Arenaria oreophila</i>	53	15 (28)	14 (26)	24



**Fig. 3.** Relationship between habitat severity, as indicated by habitat biomass, and the increase in species richness (ISR) (a) and the Relative Interaction Index (RII) calculated from species abundance data in the studied communities (b).

nurse trait effect), indicating that cushions could not completely buffer the species loss occurring in cushion-free areas. These findings are in accordance with a recent



**Fig. 4.** Mean of  $RII_{neighbors}$  at low and high environmental stress (left) and of  $RII_{environment}$  without and with cushions (right) indicating the effect of cushions on species richness at the low and high severity sites and the effect of environmental severity on species richness in cushion-free areas and cushions respectively.

meta-analysis of Michalet et al. (2014), which showed that nurse trait effects in temperate climates mainly acted to increase net competition at low-stress sites, while environmental severity effects drove increasing net facilitation at high-stress sites. At one site (BMS), the increased association between non-cushion species and cushions of *A. polytrichoides* towards higher elevations was specifically related to significantly decreased soil nutrient availability with increasing altitude (Yang et al. 2010), therefore corroborating that the buffering effect of cushions likely reduces with increasing stress, even though net facilitation increases. The net facilitation effect here increases with increasing habitat severity only, because the reduction in species richness and abundance is stronger in cushion-free areas compared to in cushions. In other words, the

increase in facilitation intensity with increasing habitat severity is solely due to an environmental severity effect, but modified in magnitude by the nurse trait effect.

### Species specificity of facilitation: a nurse trait effect

Along with the well-studied relationship between habitat severity and facilitation intensity of cushions, the importance of a cushion plant's morphology (traits) for its facilitative effects was demonstrated recently. In the Sierra Nevada Mountains, SW Spain, cushions of *A. tetraquetra* growing at higher elevation were more compact and larger, had stronger effect sizes on soil water and organic matter content and showed stronger facilitation effects than cushions at lower elevation (Schöb et al. 2013). We suggest that similar nurse trait-based effects may underlie differences in facilitation intensity among cushion species observed in our study (e.g. *A. polytrichoides* and *P. articulata* at BMS). Chen et al. (2014) reported that the difference in enhanced species richness between *A. polytrichoides* and *P. articulata* was due to the difference in nutrient conditions (P and K) under different cushion species. Similarly, in the high Andes, photochemical efficiency and reproductive output of established individuals of a non-cushion species (*Taraxacum officinale*) was higher within *Azorella monantha* cushions than within *Laretia acaulis* cushions and was related to a twofold higher K concentration in the soil beneath *A. monantha* compared to *L. acaulis* (Cavieres et al. 2008). Therefore, interspecific differences seem to be related to species differences in their capacity to alter resources and stresses in particular environments. In our study, all species studied shared the characteristic cushion morphology. Nevertheless, small differences in traits relevant for the ecosystem engineering effects of cushions may be responsible for differences in their facilitation effects.

### Are nurse trait effects the basis for deviations from the stress-gradient hypothesis?

*Thylacospermum caespitosum* in our study, growing at a high severity habitat (i.e. represented by low habitat biomass, ZGL), had only weak positive effects on species richness and even negative effects on mean species abundance (Fig. 2a,b). In contrast, for example *A. lancangensis* growing at both low and high severity habitats (i.e. represented by high and low habitat biomass, respectively, DDL and DXS) showed a strongly positive impact on species richness and mean species abundance even at the low severity site (Fig. 2a,b). Therefore, clear deviations from the general pattern of increasing facilitation with increasing severity occurred, depending on the nurse species.

Separate studies working with *T. caespitosum* at extremely high elevations (ca. 4800–5900 m) in the Indian

Trans-Himalayas (western part of the Tibetan Plateau) with a very cold and dry climate ( $<100 \text{ mm}\cdot\text{yr}^{-1}$ ) indeed showed that this exceptionally hard and compact cushion species does not provide microsites with better thermal and nutrient conditions than surrounding open areas, explaining the lack of facilitation of this species (de Bello et al. 2011; Dvorský et al. 2013). This suggests the nurse trait effect as the underlying driver of the species specificity of facilitation observed in our study. Therefore, species-specific nurse trait effects explain the deviations of individual site/species combinations from the general pattern of increasing facilitation with increasing environmental severity. Forthcoming studies in the HHM now need to analyse the interplay between the functional traits of the cushions and the environmental gradients, and their consequences for non-cushion species (Schöb et al. 2013; Michalet et al. 2014).

### Conclusion

Our results suggest that facilitation by cushion plants is key to structuring diversity and composition of natural communities at high elevations in the species-rich HHM. It is clear now that cushion plants act as nurse species as well as keystone species in these alpine habitats. Along with a 'real' stress gradient, reflected in habitat biomass, the strength of facilitation of cushions increased with increasing habitat severity. Partitioning the net effects of facilitation of cushions showed that the increase of facilitative effects of cushions on species richness with increasing habitat severity appeared to be due to changes in performance of the response species growing without cushions (i.e. an environmental severity effect). Nurse trait effects, however, modulated the intensity of facilitation. On the one hand, along the severity gradient cushions lost some capacity for environmental buffering, thereby reducing, but not eliminating, environmental severity effects within the cushion habitat. On the other hand, nurse trait effects were responsible for deviations of some species from the average effect of cushions on diversity. Despite the species specificity of facilitation by cushion plants in the HHM, their overall positive effect on species diversity indicates that cushion plants may represent efficient biotic refuges for other alpine plants when migrating to higher elevations because of global warming in the HHM. Our results clearly indicate that cushion plants will not lose their facilitative ability for non-cushion species if stress is reduced.

### Acknowledgement

Jianguo Chen and Yang Yang contributed equally to this work. We gratefully thank Cristina Armas (Almería) for her useful advice on data analysis. We thank Joelle



Hoggan for English editing of this paper. This work was supported by grants from Strategic Priority Research Program (B) of the Chinese Academy of Sciences (Grant no. XDB03030112), the Natural Science Foundation of China (NSFC) (Grant no. U1136601 to H Sun, 31360049 to Z M Li, 31470321, 31270005 to Y Yang), and The CAS/SAFEA International Partnership Program for Creative Research Teams. C. Schöb was supported by the Swiss National Science Foundation (PAOOP3\_136474 and PZOOP3\_148261). Richard Michalet (Talence) and two anonymous reviewers are thanked for their constructive comments on our paper.

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## Supporting Information

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

**Appendix S1.** Details of the 11 communities studied at the upper limit of plant distribution in the Himalayan Hengduan Mountains.

**Appendix S2.** Relationship between Habitat biomass ( $\text{g}\cdot\text{m}^{-2}$ ) and effective precipitation (EP,  $\text{mm}\cdot\text{C}^{-1}$ ) during the growing season (Jun, Jul and Aug) of 11 studies sites in the Himalayan Hengduan Mountains.

**Appendix S3.** Values of  $\text{RII}_{\text{neighbours}}$  at low and high environmental stress and of  $\text{RII}_{\text{environment}}$  with and without cushions for *Arenaria polytrichoides* at QES and BMS, *A. lancangensis* at DDL and DXS and *Potentilla articulata* at GGS and BMS.