



No evidence of facilitation collapse in the Tibetan plateau

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Keywords

Competition; Environmental stress; Facilitation; Interaction intensity; Species richness

Abbreviations

BLH = Beiluhe; TTG = Tanggula; TTH = Tuotuohe; XDT = Xidatang; RII = relative interaction index; SGH = stress gradient hypothesis

Nomenclature

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Abstract

Questions: The relative importance of facilitation under different environmental conditions has raised some recent controversy centred on predictions of the stress gradient hypothesis (SGH) for its apparent lack of predictive power under very stressful conditions. This criticism, however, is not widely shared nor fully supported by empirical data. We addressed whether changes in interaction intensity in plots under severe environmental stress determine an increase in facilitation and whether facilitation would expand the realized niche of some plant species.

Location: Four sites differing in elevation and environmental conditions along a N–S transect in the Central Tibetan Plateau, Qinghai Province, China.

Methods: We assessed plant interaction intensity between the cushion plant, *Androsace tapete*, and species growing inside its canopy. We recorded species and number of individuals in cushions and in gaps, and mass of the two most frequent species in each site.

Results: Interactions ranged from competition to facilitation, depending on environmental severity. Net interaction balance followed predictions of the SGH, from competition on the relatively more mesic sites to facilitation in the relatively more stressful sites. There were no hints of facilitation collapse even though our harsher sites posed extreme conditions for plant survival. The main limiting factor seems to be temperature, as interaction intensity responded most to this factor, rather than to elevation or rainfall.

Conclusions: Facilitation expanded the realized niche of some species, counteracting adverse environmental conditions. We found no collapse of facilitation under the most stressful conditions, even though some sites were at the edge of the distribution range for the cushion species.

Introduction

The relevant role that positive plant–plant interactions play in community dynamics has been evidenced in the last decade, and now facilitation is fully integrated into mainstream ecology (Bruno et al. 2003; Callaway 2007; Brooker et al. 2008). However, the relative importance of facilitation for species diversity under different environmental conditions has recently been challenged based on specific predictions of the SGH (Bertness & Callaway 1994), which expects facilitation to be more important under environmental stress. The SGH, although not intended to be a quantitative model, received criticism for its apparent lack of predictive power under very stressful

conditions (Maestre et al. 2005), particularly in dry environments. This criticism, however, is not widely shared (e.g. Lortie & Callaway 2006; He et al. 2013) nor fully supported by field data (e.g. Armas et al. 2011). A recent large meta-analysis showed, with strong statistical support, that the SGH held when used to predict general trends in species interactions with stress (He et al. 2013). Most criticism of the SGH involves procedures that may include confounding factors derived from experimental flaws (He & Bertness 2014).

Nevertheless, Michalet et al. (2006) found a weakening of positive effects (in terms of decreasing species diversity) towards the stressful end of an environmental gradient, which they termed the ‘collapse’ of facilitation (Michalet

et al. 2013). This decrease in positive effects exerted by one species over another could be justified by lack of resources to sustain plant life, at sites when even the nurse plant can barely survive (Michalet et al. 2013). Similarly, Malkinson & Tielbörger (2010) proposed that physiological responses are not linear regarding stress, suggesting that the importance of facilitation may be lower at both ends of a stress gradient. Indeed, at the dry end of an aridity gradient plants are limited by water, and facilitation would only occur if benefits from growing close to another species exceed competition for water (Holmgren et al. 1997; Tielbörger & Kadmon 2000) or if the benefactor species increases water availability to the facilitated species (Zou et al. 2005; Maestre et al. 2009; Prieto et al. 2010). Since increases in aridity in many areas of the world are a consequence of climate change, it is critical to clarify SGH predictions and the shape of the severity–interaction relationship to better forecast future changes in plant community structure and function (Callaway 2007).

Here, we report an observational study where we tested the effect of a cushion plant, *Androsace tapete*, on its community along an elevation gradient – overall dry – expanding from relatively moister warmer habitats to relatively drier cooler habitats in the distribution range of the species in the central Tibetan Plateau above 4300 m a.s.l. Globally, cushion plant species are found in exposed high-elevation habitats usually hosting other plant species inside their canopy, suggesting mostly facilitation processes (e.g. Núñez et al. 1999; Arroyo et al. 2003; Cavieres et al. 2006; Schöb et al. 2013; Aubert et al. 2014). Functional traits of the cushion life form buffer extreme environmental conditions, thus favouring growth of other species inside the canopy (Cavieres et al. 2006, 2007; Cavieres & Badano 2009) by creating new niche space (Schöb et al. 2012). By looking at cushion effects we can estimate facilitation intensity at the whole community level, as there are no other positive effects among plants in such high-elevation habitats (Fajardo et al. 2008).

We addressed changes in the intensity of facilitation along a gradient of strong environmental stress by sampling spatially distant populations of our target species in the central Tibetan Plateau. Low temperatures and scarce precipitation, combined with high elevations and often with thin soil, pose very harsh conditions for plant life in these environments. We expected that (1) there would be an increase in the intensity of facilitation by the cushion species on its associated community as environmental severity increased, the severity–interaction relationship being monotonic and positive with increasing aridity and decreasing productivity (Armas et al. 2011). We also expected that (2) where facilitation prevails, it expands the realized niche of species otherwise unable to survive in open habitats outside the cushion; and finally (3) effects of

cushion plants on the local environment within their canopy lead to distinct communities inside and outside the canopy, differing in composition and species richness.

Methods

Study area

We selected four sites along a north–south gradient in the central Tibetan Plateau between the KunLun Mountains in the north and the Tanggula Mountains in the south (32°50′–35°43′ N, 91°55′–94°26′ E, 4350–5500 m a.s.l.), Qinghai Province, China. The lowest and highest sites, Xidatang (4350 m) and Tanggula Pass (5350 m), were 1000 km apart, with two other sites, Tuotuohe and Beiluhe (4650 m), in between. The climate pattern is monsoonal, with rains in summer when temperatures are higher and plants grow actively. Because no long-term meteorological observations are available for the above sites except Tuotuohe, climate data (1979–2010) were extracted from the China meteorological forcing data set (0.1° × 0.1°; Yang et al. 2010; Chen et al. 2011). There is a precipitation gradient that increases from north to south, opposite to mean annual air temperature, which slightly increased towards the north as a consequence of lower elevations (Table 1).

Meteorological records from 1979 to 2010 at Tuotuohe station show a mean annual precipitation of 302 mm (range 160–536 mm) well below the 1726 mm annual pan evaporation, implying intense water stress. Most (>85%) precipitation occurs in the growing season (May to September). Mean air temperatures in the coldest and warmest months (January and July) were –16.9 and 6.9 °C, respectively, with an annual mean of –4.8 °C. Mean annual air temperature increased by 2.0 °C between 1979 and 2010, and climate is changing fast (Xue et al. 2009).

Our field sites are subject to several levels of disturbance by livestock and wild animals and to climate stress, with an additional stress factor provided by soil depth. Two of our four sites (Xidatang and Beiluhe) had relatively deep, fertile soil, while Tuotuohe and Tanggula Pass were on rocky outcrops with skeletal soils. They therefore differed in temperature, rainfall regime and soil fertility (Table 1).

Our four sites are dominated by the cushion-forming species *A. tapete* (Primulaceae), an endemic perennial herb widely distributed in high-elevation steppes and meadows in the central Tibetan Plateau (Li et al. 1985, 1987), reaching up to 5300 m a.s.l. (Li et al. 2013). Habitats colonized by *A. tapete* are also occupied by shrub and forb species such as *Androsace mariae* Kanitz, *Leontopodium pusillum* (Beauv.) Hand.-Mazz., *Poa* sp., *Polygonum sibiricum* Laxm., *Potentilla bifurca* L. and *Saxifraga* spp. Previous reports on the phylogeny, biogeography and morphological evolution of *A. tapete* (Geng et al. 2009; Zeng et al. 2010; Wang et al.

Table 1. Elevation, summer (June–August) rainfall and mean temperature (*T*), soil nitrogen (N) and organic matter (OM) in soils under *Androsace tapete* cushions and in gaps in four sites across the Tibetan Plateau in Qinghai Province, China. N and OM values are mean \pm 1SE (*n* = 50).

	Elevation (m)	Rainfall (mm)	Summer <i>T</i> (°C)	Total N (%)		Soil OM (mg·g ⁻¹)	
				Cushion	Gaps	Cushion	Gaps
Beiluhe	4640	203	4.8	0.03 \pm 0.01 ^a	0.07 \pm 0.02 ^a	4.5 \pm 1.0 ^a	5.8 \pm 0.4 ^a
Tanggula Pass	5230	318	4.1	0.33 \pm 0.02 ^c	0.29 \pm 0.03 ^c	48.9 \pm 3.9 ^c	53.2 \pm 3.6 ^c
Tuotuohe	4650	212	5.9	0.34 \pm 0.03 ^c	0.33 \pm 0.03 ^c	59.2 \pm 5.8 ^c	54.6 \pm 5.7 ^c
Xidatang	4365	122	6.1	0.18 \pm 0.02 ^b	0.16 \pm 0.02 ^b	25.2 \pm 2.1 ^b	25.4 \pm 2.4 ^b

Values in a column with the same superscript letter are not significantly different (*P* > 0.05).

2013) suggest it plays an important role in the formation and evolution of Tibetan steppes and meadows, and can be considered a foundation species (*sensu* Ellison et al. 2005) due to its community-level effects. Cushions in our field sites were randomly distributed and surrounded by open areas, with cover ranging from 1.3% to 5.0%, and hosted annual and perennial species within their canopies.

Sampling design

At each of our four sites we sampled 50 cushions and 50 paired open areas equal in size to that of cushions within an area of about 500–1000 m². Cushion size was calculated as the area of an ellipse by measuring the largest diameter and its perpendicular. Cushion shape was simulated with wire, and the wire randomly placed near the cushion for sampling the paired open area. In summer 2012, the number of individuals of all vascular plants within each cushion and the associated gap was recorded. We recorded individuals and species as the effects of foundation species may influence both independently. Total number of species found over all four sites was 53.

For species common to all four sites, preferences (cushion, gap) were estimated as the percentage distribution of individuals between these two habitats.

At each site, soil samples (0- to 5-cm depth) beneath ten cushions and ten paired gaps were collected for chemical analysis. Samples were air-dried and soil organic matter (OM) content (g·g⁻¹ soil) was determined as mass loss after ignition at 400 °C for 24 h. Nitrogen was determined using Kjeldhal analysis and P with colorimetry.

Two individuals of the two most frequent species at each site were sampled across ten cushions and ten paired gaps. For grasses, we sampled tillers, as whole plants were difficult to separate from cushions, while whole individuals were sampled in the case of forbs. Samples were dried at 70 °C for 48 h and weighed.

Data analysis

We calculated the intensity of the interaction between *A. tapete* and its associated community as a function of

number of individuals, number of species and individual plant mass, and the frequency of facilitation as the number of facilitated species. We used the relative interaction index (RII; Armas et al. 2004) to assess interaction intensity in terms of individual (RII_{indiv}) and species number (RII_{sp}), as well as plant mass (RII_b). RII is a useful metric because plant species in the herbaceous community differ among field sites and can have disparate sizes irrespective of resource availability, making plant biomass not directly comparable among sites or species.

Interaction intensity was calculated for each paired cushion and open plot as

$$RII = \frac{N_c - N_o}{N_c + N_o}$$

where *N_c* is species richness (RII_{sp}), the number of individuals (RII_{indiv}) or individual plant mass (RII_b) in the cushion and *N_o* is the equivalent value in the open.

Frequency of facilitation was estimated as the number of species for which RII_{indiv} > 0.1.

Differences in soil N and OM between microhabitats and among sites were tested with two-way ANOVA. Statistical analyses to test for the effects of site and habitat type on species richness and plant density were performed using mixed linear models, with habitat type as fixed factor and site as random factor. We tested several variance structures to avoid heteroscedasticity and selected the best one (in our case varIdent, i.e. constant variance structure) by comparing them via Akaike information criterion. We applied Bonferroni correction for multiple *post-hoc* comparisons. Relationships between variables were tested by regression analysis. All calculations and statistical analyses were performed with the InfoStat software package (Di Rienzo et al. 2008).

Results

Climate and soil

Annual rainfall is low and concentrated in summer (Fig. 1), when July temperatures range between 12 and

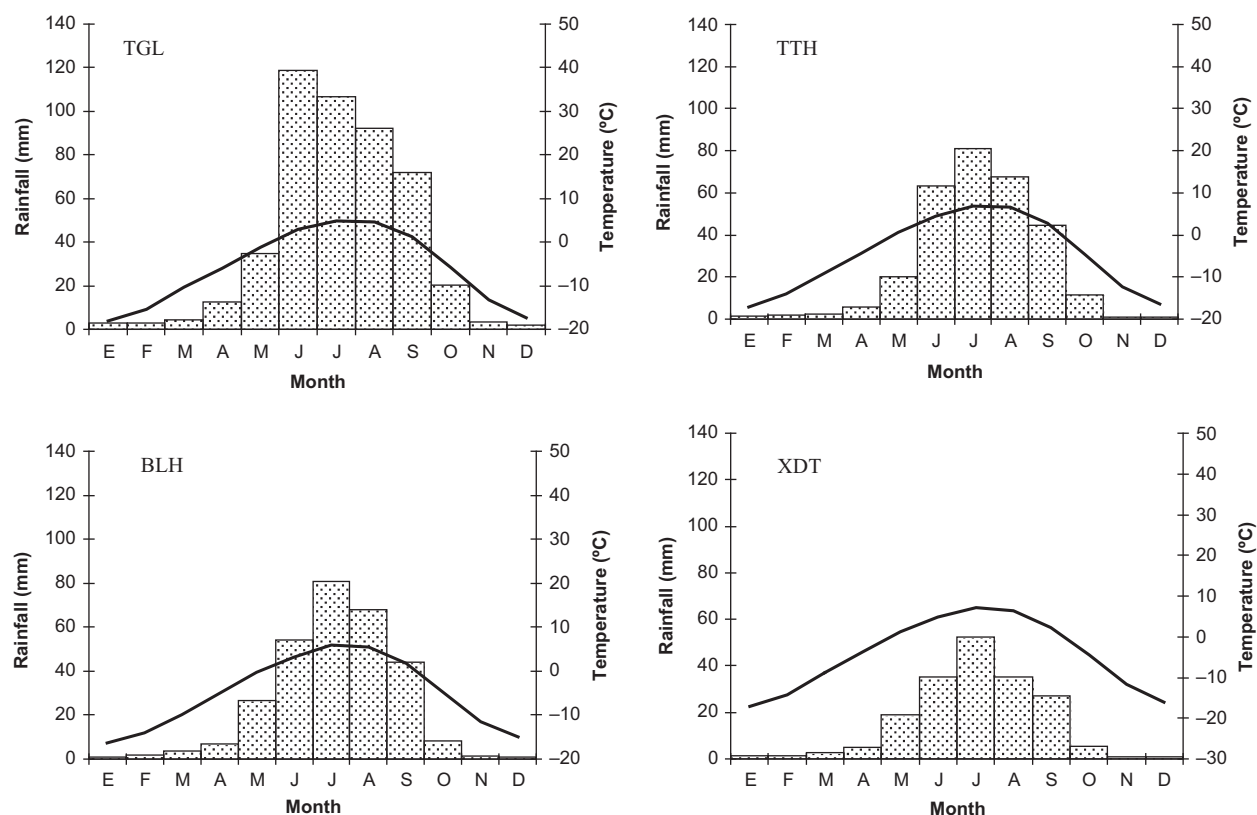


Fig. 1. Climate diagrams of Tanggula (TGL), Tuotuohe (TTH), Beiluhe (BLH) and Xidatang (XDT) field sites in central Tibetan Plateau, Qinghai Province, China.

Table 2. Data on canopy (cushion) size, species and number of individuals inside the canopy and in paired gaps, and relative interaction index for species ($R_{II_{sp}}$) and individual ($R_{II_{indiv}}$) number in the cushion species *Androsace tapete* in four field sites across the Tibetan Plateau in Qinghai Province, China.

	Cushion size (cm ²)	Species in cushions	Species in gaps	Individuals in cushions	Individuals in gaps	$R_{II_{sp}}$	$R_{II_{indiv}}$
Beiluhe	247.85 ± 18.81 ^a	2.74 ± 0.22 ^b	1.98 ± 0.22 ^b	7.82 ± 2.93 ^b	4.92 ± 2.17 ^c	0.16 ± 0.05 ^a	0.20 ± 0.06 ^a
Tanggula Pass	68.30 ± 17.51 ^b	2.54 ± 0.22 ^b	2.50 ± 0.22 ^b	6.96 ± 2.93 ^b	4.90 ± 2.17 ^c	0.03 ± 0.05 ^a	0.13 ± 0.06 ^{ab}
Tuotuohe	83.30 ± 10.74 ^b	2.20 ± 0.20 ^b	2.60 ± 0.20 ^b	10.63 ± 2.68 ^b	14.20 ± 1.98 ^b	-0.08 ± 0.04 ^b	-0.13 ± 0.05 ^c
Xidatang	199.10 ± 20.97 ^a	4.41 ± 0.21 ^a	5.31 ± 0.22 ^a	39.37 ± 2.90 ^a	39.49 ± 2.14 ^a	-0.11 ± 0.05 ^b	-0.06 ± 0.05 ^{bc}

Values are mean ± 1SE ($n = 50$). Values in a column with the same superscript letter are not significantly different ($P > 0.05$).

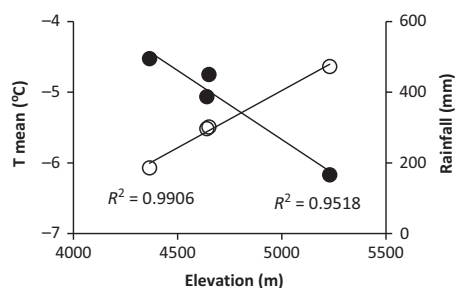


Fig. 2. Climatic gradients across the central Tibetan Plateau. Mean annual temperature (solid dots) and rainfall (clear dots) change with elevation with opposite patterns.

18 °C in our highest (Tanggula) and lowest (Xidatang) sites. The southernmost sites (Tanggula and Tuotuohe) had much more soil OM and soil N content than the two northern sites (Table 1). They had, nevertheless, smaller cushions (Table 2) likely due to higher elevation and lower temperature (Fig. 2). In addition, and perhaps because of higher temperatures, soil N tended to increase from the southern sites to the northern sites. Differences in soil properties were high between Beiluhe and all other sites, cushion microhabitats having slightly higher, although not significant, soil nutrient content than open areas (Table 1).

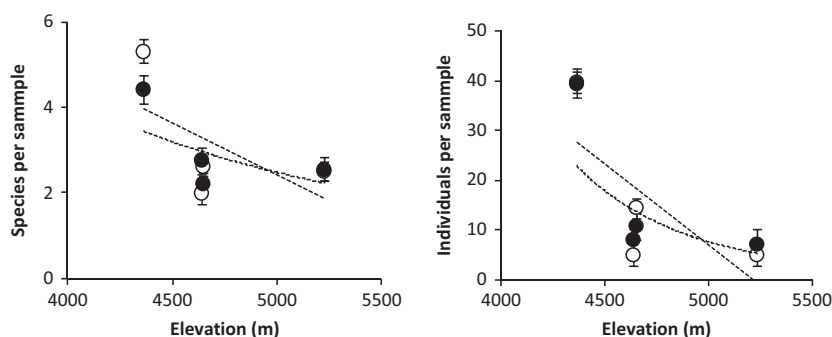


Fig. 3. Species and individual number in cushions and open plots tend to decrease with elevation, but not in a significant manner ($P > 0.05$). Values are means ($n = 50$); error bars shown if larger than symbol.

Species richness and plant density

Total species number at each site ranged between 16 and 25, and was unrelated to elevation ($r = -0.34$, $P > 0.05$), showing roughly similar low numbers in all four sites. Species richness, i.e. the number of species within a plot (cushion or similar area in gaps), differed significant only between Xidatang, the lower site, and the other three sites, both in gaps and within cushions (Table 2), and did not change with elevation (Fig. 3). The number of individuals growing in gaps and in cushions tended to decrease with elevation ($r = -0.7$ for both, $P > 0.05$) but the trend was not significant, perhaps due to the small number of points (Fig. 3), and was less pronounced within cushions than in gaps.

Species richness within an individual cushion ranged between zero and 13, and the number of individuals per cushion between zero and 150. However, species or individual numbers in cushions were unrelated to cushion area ($P > 0.05$), as larger cushions did not necessarily host more species or individuals. There was a weak relationship between species richness in gaps and in cushions, so that

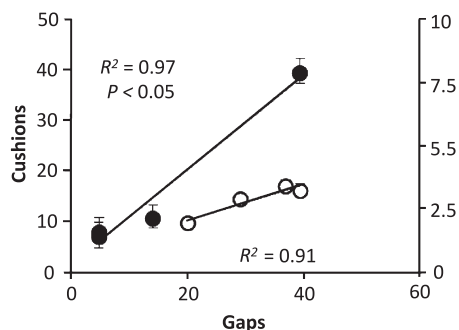


Fig. 4. Relationship between number of individuals (solid dots; left y-axis) and species richness (clear dots; right y-axis) in gaps and in cushions in our four field sites. Values are means ($n = 50$); error bars shown if larger than symbol.

the more species in gaps, the more species in cushions, and a strong relationship regarding number of individuals (Fig. 4), suggesting that they were related to environmental conditions. There may be, however, a confounding factor related to cushion age, which we did not consider.

Cushions in Beiluhe and Tanggula had overall more species and individuals than open habitats, a pattern reversed in Tuotuohe and Xidatang (Table 2). Considering only common species present at all sites, there were contrasting patterns between cushions and gaps regarding habitat preference, particularly between Tanggula and Tuotuohe, the two southern sites. At Tuotuohe, 6% of species were more abundant in cushions, 50% more abundant in gaps and 44% equally abundant in cushion and open habitats. By contrast, in nearby Tanggula, 33% species were more abundant in cushions vs 5% more abundant in gaps, while most species (62%) were equally abundant in cushion and open habitats. In the relatively warmer site, Xidatang, 20% of species were found in cushions, 28% in gaps and 52% occupied both habitats. Percentage species in gaps increased with increasing June temperature ($r = 0.83$, $P < 0.05$), suggesting that cushions buffered climatic extremes. Less common species balanced these numbers, so that overall patterns were less clear.

Considering the number of individuals, interaction intensity (R_{indiv}) differed among sites, ranging from facilitation in Beiluhe, a relatively colder site, to competition in Xidatang (Fig. 5), which is relatively warmer. Facilitation was more frequent in Beiluhe, where positive R_{indiv} included 61% of species, and less frequent in Tuotuohe (24.5%) and Xidatang (27.4%). Facilitation frequency was negatively correlated to soil N ($r = 0.93$, $P < 0.05$). Regarding species, RII was only slightly different in Xidatang and Tuotuohe, but ranged from facilitation in Beiluhe to competition in Xidatang (Fig. 5). Therefore, Tuotuohe and Xidatang appeared as the less environmental-demanding sites while Beiluhe and Tanggula were the most stressful sites because of low temperatures.

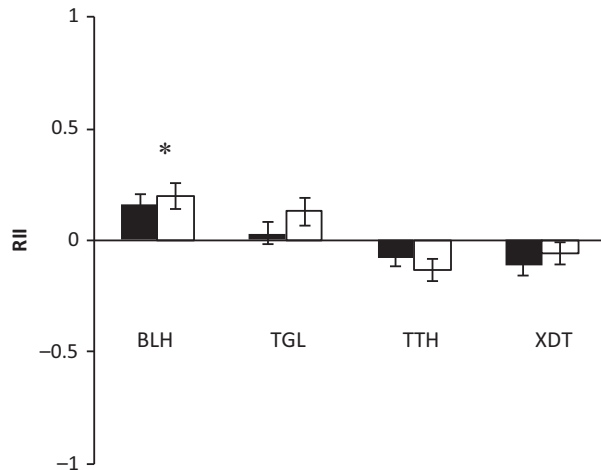


Fig. 5. Relative interaction index (RII) applied to species richness (solid bars) and individual numbers (clear bars) at Beiluhe (BLH), Tanggula Pass (TGL), Tuotuohe (TTH) and Xidatang (XDT). Values are mean \pm 1SE ($n = 50$). Bars with * are significantly different from zero.

There was a slight change in interaction intensity, as RII_{indiv} tended ($P = 0.1$) to decrease with increasing June temperature (Fig. 6a), i.e. to increase competition in more mesic sites, and both RII_{sp} and RII_{indiv} were unrelated to elevation (Fig. 6b). The only point in common between Beiluhe and Tanggula is colder summers (Table 1), 1–2 °C below the other two sites, as they differed in rainfall and, above all, soil characteristics.

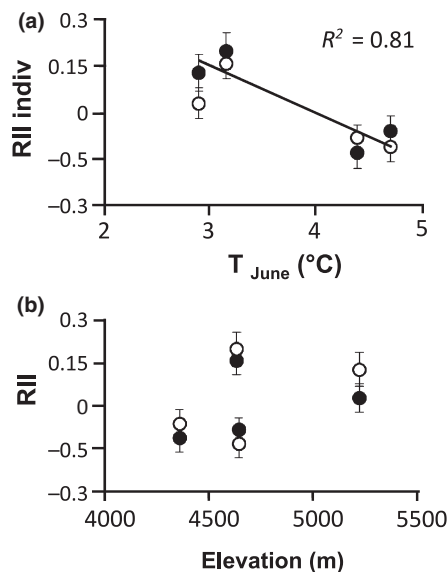


Fig. 6. Facilitation effect on individuals number (RII_{indiv}) tended to decrease ($P = 0.1$) with increasing temperature in June (a) but did not affect RII_{indiv} or RII_{sp} with elevation (b). Values are means ($n = 50$); error bars shown if larger than symbol.

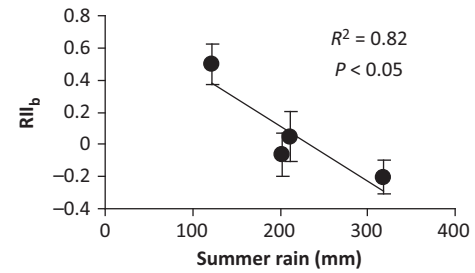


Fig. 7. Relationship between RII of biomass of most common species and summer rainfall.

Mean plant size of the two most abundant species in each site was higher in the two northernmost sites, and followed a pattern similar to cushion size. Interaction intensity based on biomass of the two most abundant species in each site decreased with increasing water availability, changing from positive (facilitation) to negative (competition) as summer precipitation increased (Fig. 7).

Discussion

As expected, we found an increase in the intensity and, to a lesser extent, the frequency of facilitation by cushion species on the associated community as environmental severity increased. Our data showed competition at Xidatang, the relatively warmer site, and facilitation at Tanggula Pass, a relatively cooler site. Facilitation was most intense, however, at Behilue, a site north of Tuotuohe, with lower rainfall and more soil nutrients but colder summers. The environment was overall stressful in all sites due to low temperature, high irradiance and lack of water, which independently influence habitat severity (Mod et al. 2014). However, in this framework it was possible to establish differences in environmental harshness within which plant interactions are generally consistent with the original formulation of the SGH. We did not find a collapse of facilitation in the most stressful sites, as suggested by He et al. (2013). We did find competition in Tuotuohe, a quite harsh site, but facilitation prevailed further south and higher up in Tanggula, reflecting the fact that plant–plant interactions depended on microsite characteristics (Kikvidze et al. 2011). Tanggula and Behilue had in common colder summers, on average 1–2 °C below the other two sites. Such temperature differences notably influence plant performance (Li et al. 2013) and may suffice to explain the recorded changes. Tanggula and Beiluhe also showed the highest frequency of facilitated species, but this could be masked by climatic conditions. Although cushions can increase soil OM and nutrients (Schöb et al. 2012, 2013; Anthelme et al. 2012) as well as soil water availability

(Schöb et al. 2012, 2013; Anthelme et al. 2012), in this case the main effect seems to be buffering temperature extremes (Körner 2003; Cavieres et al. 2006) because of the cushion thick canopy.

Several authors (e.g. Maestre et al. 2005; Michalet et al. 2006, 2013; Soliveres & Maestre 2014) predicted a ceasing of positive effects of nurse plants under tough environmental conditions, when potential benefactor species may actually not act as nurses. However, our data overall support the original SGH, with facilitation predominating at the most stressful sites and competition at the more mesic sites. Our data suggest that harshness here was more related to temperature than to rainfall or elevation, which agrees with empirical evidence supporting the SGH both in alpine (Cavieres et al. 2000; Callaway et al. 2002; Schöb et al. 2012) and dry environments (Pugnaire & Luque 2001; Armas et al. 2011), contrary to some conceptual or statistical (meta-analyses) papers, which suggest a collapse of facilitation in extreme environments.

We could ask whether our sampling sites included really extreme environments, and the answer is yes. Not only overall rainfall was low (186–473 mm in our four sites) but temperatures were rather low (annual mean -4.5 to -6.2 °C) and elevations high (>4300 m). Although difficult to model without actual measurements (Nobel 1991), CO_2 partial pressure decreases with elevation, and stomatal conductance must increase to continue to fix CO_2 at the expense of water loss (Nobel 1991). Low soil temperatures inhibit stomatal opening (Carter et al. 1988), and transpiration generally decreases with elevation, but overall gas exchange efficiency is low at high elevations (Körner 2003). Therefore, water transpired by *A. tapete* per unit C fixed in Tanggula, at 5320 m, should be higher than in Xidatang, at 4365 m, since temperature has little influence on the process, placing plants in Tanggula under extreme stress conditions and at the edge of the elevational distribution (Li et al. 2013). Even then, *A. tapete* was able to exert positive effects on its associated species, increasing the number of individuals per unit area over nearby gaps, although it did not host more species as the strong climate filtered the number of species reaching such elevations. Our results may have been influenced by grazing, which we did not estimate; however, we do not expect a bias regarding herbivory as livestock (yak, sheep, horse) and wild animals (deer, donkey) were quite frequent and randomly distributed all over the area (Harris 2010).

Paradoxically, the two northernmost sites had the larger cushions but were also the driest and had the lowest levels of soil N and OM. These values were unrelated to interaction intensity, suggesting that soils did not exert a strong effect on the positive effect of *A. tapete* on its associated species. As in other dry mountains (Cavieres et al. 2006;

Schöb et al. 2012), there was a crossed environmental gradient as temperature increased while rainfall decreased with elevation. Nitrogen and OM were much higher in the southernmost, higher elevation sites. As in one of these sites (Tanggula) we found facilitation, with competition in the other (Tuotuohe), it could be argued that soil properties do not drive interactions in this environment as they do in other dry systems (Pugnaire et al. 2004). Since soil OM and N are correlated, there was a trend ($P = 0.1$) to increase RII with decreasing temperature, pointing to an interaction shift, as in other alpine systems (Callaway et al. 2002; Schöb et al. 2012; Cavieres et al. 2014). In the same direction point the interaction intensity including biomass of the most frequent species, which changed from positive under lower summer precipitation to negative under relatively more rainfall. Accumulation of soil N and OM at relatively higher elevations may suggest that soil processes are halted at some point by low temperatures.

Cushion species change the environment within their canopy and create conditions that increase available niche space (Schöb et al. 2012), allowing facilitated species to expand their geographic range and colonize sites otherwise out of reach. Environmental changes induced by cushions are as important as climate for the distribution of species growing within their canopies (Cavieres et al. 2014). However, such positive effects depend on the physiological status of the nurse (Schöb et al. 2013), and may decrease as the nurse departs from its physiological optimum. In the Sierra Nevada, Spain, Schöb et al. (2013) found that positive effects were more intense at higher than at lower elevations, because the nurse species, *Arenaria tetraquetta*, had a compact growth habit at high elevations that protected subordinate species very efficiently under harsh conditions. In contrast, at low elevations, *Arenaria tetraquetta* growth form was loose and its positive effects less pronounced (Schöb et al. 2013). Growth of *A. tapete* cushions was not much influenced by the harsher conditions in the two southern sites, as differences in canopy size were not significant. Therefore, it seems that physiological stress did not play a major role in the positive effects of *A. tapete* in our field sites.

We hypothesized that positive effects of cushions would lead to distinct communities inside and outside their canopies, differing in composition and species richness. Although, overall, the proportion of widespread common species living in gaps increased with increasing temperature in June, suggesting that cushions protected against climatic extremes (Körner 2003), we obtained a range of results, from sites where many species preferred cushions (Tanggula) to sites where they preferred gaps (Tuotuohe), with other sites in between. Therefore our hypothesis is generally supported. Tanggula and Tuotuohe are close to each other and share a similar climate, with higher rainfall

than the other two sites further north. Tanggula, however, at 5300 m a.s.l., clearly represents the most stressful site of the four sites, as discussed above, but *A. tapete* cushions hosted more common species within their canopy than in any other site, lending support to our hypothesis that collapse did not happen here. In fact, species richness in Tanggula was higher (21) than in Tuotuohe (16), while mean number of species per cushion was about the same.

We also hypothesized that facilitation expands the realized niche of species otherwise unable to survive in the open. This is supported by Tanggula data, which at 5230 m a.s.l. show a greater proportion of species preferring the cushion, and indirectly by Tuotuohe data (4600 m), which had the lowest species richness in what may be related to the small role of cushions acting as nurses. The slightly higher summer rainfall and higher summer temperature may make Tuotuohe a more mesic place where competition prevails, as opposed to Tanggula (Fig. 5).

In summary, our data do support the SGH, since facilitation increased as the environment became harsher, and even slight environmental improvements released competition. Consequently, we did not find a collapse of facilitation at the most stressful environments, even though we included very severe sites for plant survival among our field sites. As expected, facilitation expanded the realized niche of some species and was almost as important as climate in influencing this distribution (Cavieres et al. 2014).

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