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

Chen, Jianguo ; Schöb, Christian ; Zhou, Zhuo ; Gong, Qiangbang ; Li, Xinhui ; Yang, Yang ; Li, Zhimin ; Sun, Hang

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.

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1 **Cushion plants can have a positive effect on diversity at high elevations**
2 **in the Himalayan-Hengduan Mountains**

3

4 **Running head: Facilitation of cushions at high elevations**

5

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26

27 **Abstract**

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

33 **Location:** 11 alpine plant communities dominated by cushion plants in the
34 Himalayan-Hengduan Mountains, within the mountain system of
35 southern-central China.

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

44 **Results:** The presence of cushion plants increased species richness and
45 abundance in most studied plant communities. The net facilitation effect of
46 cushions increased with increasing habitat severity, an effect that could be
47 attributed mainly to a reduction in species richness in cushion-free areas with
48 increasing severity. However, the changes in magnitude of facilitation of

49 particular cushion species growing in high and low severity habitats could be
50 attributed to both environmental severity and neighbor trait effects. Despite the
51 overall positive effect of cushion plants on plant species richness, not all
52 cushion species contributed to higher species richness. The deviation of
53 individual cushion species from the general pattern of increasing facilitation
54 with increasing severity indicated the species-specificity of facilitation
55 depending on the traits of nurse species.

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

63

64 **Keywords**

65 alpine habitats; cushion plants; environmental severity; facilitative interactions;
66 Himalayan-Hengduan Mountains; nurse trait effects; species richness

67

68

69 **Introduction**

70 Mountain systems support approximately one third of terrestrial plant diversity
71 (Barthlott et al. 1996). Within mountain regions, the alpine zone, located above
72 the climatic treeline and below the permanent snow line, supports around
73 8000-10000 higher plant species, accounting for ca. 4% of all known higher
74 plant species (Körner 2003). Results from comparison of ten different Asiatic
75 mountains and the European Alps indicated that the alpine flora seems to
76 represent about one fifth to one fourth of the total regional flora including that
77 found on the plateau of those regions (Agakhanjanz & Breckle 1995; Körner
78 2003). Indeed, many alpine regions are considered to be biodiversity hotspots.
79 The high degree of plant diversity in mountain areas has mainly been
80 attributed to abiotic factors, such as geographic isolation, tectonic uplift and
81 strong microhabitat differentiation (Packer 1974; Agakhanjanz & Breckle 1995;
82 Körner 1995). The role of biotic factors (facilitation/competition) in structuring
83 plant communities at high elevations has received some recent attentions
84 (reviewed by Anthelme et al. 2014). In a global set of experiments in mountain
85 plant communities, Callaway et al. (2002) drew the general conclusion that,
86 while competition commonly dominates interactions at low elevations,
87 interactions between plant species at high elevations, where abiotic stress is
88 high, are predominately facilitative. These facilitative effects have strong
89 influences on the local diversity of plant communities in alpine regions (e.g.
90 Kikvidze et al. 2005; Cavieres & Badano 2009; Butterfield et al. 2013; Cavieres

91 et al. 2014). Such positive effects of facilitating species through their effects on
92 the local environment may also be relevant for the impact of ongoing
93 environmental changes, such as climate change, on biodiversity. Facilitating
94 species may provide efficient biotic refuges for up-migrating plants during
95 primary succession of newly available areas (Anthelme et al. 2014).
96 Understanding facilitation is, therefore, not only crucial for understanding
97 current biodiversity of alpine plant communities but also for predictions of
98 alpine plant community responses to a changing climate (Anthelme et al.
99 2014).

100 The mountains of south-central China are one of the most biologically rich
101 temperate regions on earth (Sherman et al. 2008). Within this unique area, the
102 Himalayan-Hengduan Mountains (HHM, N24°40'–34°00' and E96°20'–104°30',
103 Li 1987, Fig. 1), oriented north–south along the eastern flanks of the
104 Himalayas and southeast of the Qinghai Tibetan Plateau, have been identified
105 as a hot spot for temperate biodiversity (Mittermeier et al. 1999), supporting
106 the globally richest alpine flora (Xu et al. 2014a). It is reported that the alpine
107 subnival belt (ca. 4300 – 5200 m) between the upper alpine belt and the nival
108 belt in HHM harbor over 900 truly alpine species (Xu et al. 2014a). In addition,
109 a quantitative assessment of the alpine flora across areas in the southeast
110 HHM indicated an average of 59 species per 60 m² (Sherman et al. 2008). The
111 high degree of plant diversity in this region is related to its location at a
112 biogeographical convergence zone of temperate and tropical areas and its

113 monsoonal climate (reviewed by Xu et al. 2014b). However, to our knowledge,
114 the role of biotic processes, particularly facilitation, in structuring patterns of
115 plant community diversity at high elevations in the HHM remains unclear.

116 One prominent example of facilitative interactions among plant species
117 involves organisms referred to as ‘nurse species’ (also called ‘engineering
118 species’ by Jones et al. 1994, 1997), which alter the distribution of material and
119 energy in the abiotic environment through non-trophic and trophic interactions,
120 thus creating and maintaining new habitat patches in the landscape (Jones et
121 al. 1994, 1997; Molenda et al. 2012). Within high alpine regions, species that
122 have a cushion morphology often act as ‘nurses’ due to their ability to
123 moderate environmental conditions with respect to temperature, water and soil
124 nutrition (e.g. Molina-Montenegro et al. 2006; Cavieres et al. 2007; Cavieres et
125 al. 2008; Yang et al. 2010). Such species, therefore, play an important role in
126 structuring alpine plant communities at both regional (e.g. high Andes, Badano
127 & Cavieres 2006 a, b; Cavieres & Badano 2009) and global scales (Butterfield
128 et al. 2013; Cavieres et al. 2014). Cushion plants are also occurring in the
129 alpine belt of the HHM, where previous single-site studies showed positive
130 effects of cushion species on other plant species (Yang et al. 2010; Chen et al.
131 2014). However, in order to understand the context-dependence of this
132 facilitative effect of cushions on species diversity in the HHM, a large-scale
133 sampling to assess the effects of cushion plants on plant diversity is needed.
134 This would reveal the relative importance of facilitation for species diversity

135 across environmental gradients in the HHM and allow estimating the relevance
136 of nurse species for biodiversity under climate change scenarios.

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

156

157 **Methods**

158 *Study areas and target cushion species*

159 The climatic pattern of the HHM is characterized by a monsoon with wet
160 summer and dry winter. There is a general trend of decreasing annual mean
161 temperature from south to north with values from 0 to over 20°C and the
162 minimum value and maximum value generally occur in January and July,
163 respectively (Zhang et al. 1997). Similar to temperature, annual precipitation
164 tends to decrease from south to north with values between 300 and 1300 mm
165 mostly concentrated during the summer (early June – late September) (Zhang
166 et al. 1997). In this region, alpine meadow commonly occurs at 4000 – 4500 m
167 a.s.l, with scree slopes at higher elevations. Permanent snow and ice occurs at
168 c. 5200 m.

169 A total of 11 alpine plant communities dominated by cushion species, at
170 eight different sites, were selected (Fig. 1). From north to south, we sampled
171 *Sibbaldia tetrandra* at Zhaqing snow mountain pass in northern HHM; both
172 *Chionocharis hookeri* and *Arenaria polytrichoides* at Queer snow mountain
173 pass in western HHM; *Thylacospermum caespitosum* at Zhuogela snow
174 mountain in northeastern HHM; both *A. lancangensis* and *A. densissima* at
175 Dongdala snow mountain in central HHM; *Potentilla articulata* at Gongga snow
176 mountain in southwestern HHM; *A. lancangensis* at Daxue snow mountain in
177 southeastern HHM; both *P. articulata* and *A. polytrichoides* at Baima snow
178 mountain in southeastern HHM; *A. oreophila* at Yulong snow mountain in

179 southern HHM. All 11 communities are in early successional stages and
180 characterized by open plant communities with patchy vegetation (Li et al.
181 1981). The selected target species dominated the selected plant communities
182 in the study region. Although very little is known about the growth rate of each
183 studied cushion species, it has been suggested that large cushions may have
184 taken decades or even longer time to reach their present size and may yet
185 continue to live for a long period of time due to their high rates of survival
186 (Morris & Doak 1998; Kleier & Rundel 2004).

187 As a highly stress-tolerant species, cushions often dominate at the upper
188 limit of alpine vegetation, particularly on bare soils, windswept habitats or
189 glaciated margins characterized by poor nutrient availability and cool
190 environments (Körner 2003). Assuming an upward migration of plants into
191 higher elevations due to the effects of global warming (Baker and Moseley
192 2007) and a potential relevance of facilitation by cushion plants for this shift
193 (Anthelme et al. 2014), the sampling sites were chosen to be located as close
194 as possible to the upper altitudinal limit of the cushion distributions. This
195 allowed us to examine the facilitative effect of the cushion plants on other plant
196 species at the leading edge of the expected migration process. By choosing
197 the upper altitudinal limits of the cushion plants as study sites we also avoided
198 rangeland and therefore minimized possible disturbances from human-related
199 activities (e.g. pasturing) in this otherwise heavily pastured region of the
200 Qinghai-Tibetan Plateau (Miehe et al. 2011; Haynes et al. 2013) (see

201 Appendix S1 for detailed information about the study sites and sampling
202 intensities).

203

204 *Sampling of species in cushions and cushion-free areas*

205 At each study site, we randomly selected individual cushions (with no
206 senescent or damaged parts) and followed the protocol by Cavieres et al.
207 (2014) for the plant diversity sampling. All plants growing within the selected
208 cushions were identified to species level and the number of individuals of each
209 species was counted. Since cushions are usually elliptical, we also measured
210 the longest and shortest axes of each cushion in order to estimate its area. To
211 obtain comparable samples of species in surrounding open areas, the shape
212 of each sampled cushion was replicated using a wire ring. These rings were
213 randomly placed in open areas at least one meter away from cushions, then all
214 plant individuals within the wire rings were identified to species level and the
215 number of individuals counted. In addition, we collected all of the aerial parts of
216 species within the cushion patches and in the equivalent sampled open areas.
217 All samples were stored in paper bags (one bag per plot). The bags were then
218 placed in a drying oven at 75°C for 40 h before being weighed to determine the
219 aboveground total dry biomass of plants within each sample. The biomass
220 data in cushion-free areas at each study site were averaged and used as an
221 indicator of environmental severity (see below).

222

223 *Comparison of species richness and species abundance between cushions*
224 *and cushion-free areas*

225 To compare species richness of different habitat types (i.e. cushion and
226 cushion-free areas), we generated a species \times samples matrix for each habitat
227 type in each site, where each cell (i, j) contained the abundance of the i th
228 species in the j th sample; we used this to determine the effect of cushion
229 plants on species richness within and outside cushions in each of the 11
230 communities. From the matrices, 500 samples were randomly drawn, with
231 replacement, for each sample size (from one sample to the maximum number
232 of samples); then the species richness of the 500 samples was calculated
233 using Coleman's algorithm (Coleman et al. 1982). To avoid bias due to
234 differences in the samples that were replaced, we ran the rarefaction analysis
235 for cushion and cushion-free areas at each site 20 times. Maximum likelihood
236 estimates of species richness for cushions and cushion-free areas at the
237 asymptote of the sample-based rarefaction curves were averaged and plotted.
238 The rarefaction analyses were carried out with EstimateS v. 9.01 software
239 (Colwell 2000). The increase in species richness for each studied community
240 due to the presence of a cushion species (ISR) was calculated as $ISR =$
241 $[(S_c - S_o)/S_o] \times 100\%$, where S_c and S_o are estimated values for species
242 richness in cushion and open (cushion-free areas) plots respectively at the
243 asymptotes of sample-based rarefaction curves (Cavieres et al. 2014).

244 In order to examine the impact of cushions on the abundance of

245 non-cushion species, we calculated the Relative Interaction Index ($RII_{abundance}$)
246 for each non-cushion species in each community (Armas et al. 2004).
247 Following the protocol of Cavieres et al. (2014), $RII_{abundance} = (\# \text{ within cushion}$
248 $\text{species} - \# \text{ in open area}) / (\# \text{ within cushion species} + \# \text{ in open area})$, where #
249 indicates the number of individuals of each non-cushion species. Thus,
250 $RII_{abundance} = 1$, when all individuals of a species occur within cushions;
251 $RII_{abundance} = 0$, when all individuals of a species are distributed equally
252 between cushions and open areas; and $RII_{abundance} = -1$, when all individuals of
253 a species occur within cushion-free areas. Mean $RII_{abundance}$ across all species
254 within a community was then used as an estimate for the average effects of
255 the cushion species on other plant species at that site (Cavieres et al. 2014). In
256 addition, the proportion of species unique to cushion habitats and cushion-free
257 areas was also determined in each community.

258

259 *Relationship between habitat severity and the effect size of facilitation by*
260 *cushion species*

261 Habitat severity can be reflected by habitat productivity (biomass per area and
262 unit time, $\text{g m}^{-2} \text{ yr}^{-1}$), with the latter been shown to be positively related to
263 habitat biomass under stressful conditions (Noy-Meir 1975; Weiner 2001). In
264 order to test whether there is a relationship between habitat biomass and
265 environmental severity in our study, we assessed the relationship of habitat
266 biomass with Effective Precipitation (EP; de Martonne 1927) during the

267 growing season (June, July and August) of each site. EP has been used
268 previously as a surrogate of environmental stress (Kikvidze et al. 2006;
269 Cavieres & Badano 2009), because it is generally highly correlated with habitat
270 productivity (Stadler 2005). Indeed, habitat biomass was highly correlated with
271 EP in our study ($r = 0.631$, $P = 0.037$, Appendix S2).

272 To explore the relationship between habitat severity and the facilitative
273 effects of cushion plants, we examined the correlation between ISR and mean
274 $RII_{abundance}$ and habitat biomass (aboveground biomass in cushion-free areas,
275 $g\ m^{-2}$, log transformed) across all studied communities using Spearman's rank
276 correlation implemented in SPSS.

277

278 *Environmental severity effect and nurse trait effect in facilitation of cushion* 279 *species*

280 The relative effect of the environment and nurse traits on changes in the
281 cushion effect size on species richness along the severity gradient was
282 assessed by calculating $RII_{environment}$ and $RII_{neighbors}$ as suggested by Michalet
283 et al. (2014) for three cushion species inhabiting both high (low severity) and
284 low (high severity) biomass habitats (i.e. *A. polytrichoides*: QES vs. BMS; *A.*
285 *lancangensis*: DDL vs. DXS; *P. articulata*: GGS vs. BMS). $RII_{neighbors} = (\# \text{ with}$
286 $nurse - \# \text{ without nurse}) / (\# \text{ with nurse} + \# \text{ without nurse})$, $RII_{environment} = (\# \text{ at}$
287 $low \text{ biomass habitat} - \# \text{ at high biomass habitat}) / (\# \text{ at low biomass habitat} + \#$
288 $at \text{ high biomass habitat})$, where # indicates species richness. $RII_{neighbors}$ was

289 calculated separately for high and low stress habitats, indicating the effect size
290 of cushions on species richness at high and low severity habitats respectively,
291 with $RII_{\text{neighbors}}$ below 0 pointing towards competition and above 0 indicating
292 facilitation. In contrast, $RII_{\text{environment}}$ was calculated separately for species
293 growing with and without cushions respectively, indicating the effect size of
294 environmental severity on species richness either when growing with or
295 without nurse, with $RII_{\text{environment}}$ below 0 indicating higher species richness at
296 the low severity habitat and above 0 indicating higher species richness at the
297 high severity habitat (Michalet et al. 2014). If there is a significant change in
298 $RII_{\text{neighbors}}$ between low and high stress habitats, then $RII_{\text{environment}}$ can be used
299 to attribute the change in the effect size of facilitation along the severity
300 gradient to an environmental severity effect (if $RII_{\text{environment}}$ without cushions is
301 significantly different from 0), to a nurse trait effect (if $RII_{\text{environment}}$ with cushions
302 is significantly different from 0) or to a combined environmental severity and
303 nurse trait effect (if $RII_{\text{environment}}$ with and without cushions are significantly
304 different from 0) (Michalet et al. 2014). The results of each index of the three
305 species were averaged and a Paired Sample T-test in SPSS was used to
306 examine the difference in $RII_{\text{neighbors}}$ between high and low stress habitats and
307 $RII_{\text{environment}}$ between cushion and open habitats, and One Sample T-tests were
308 used to examine the difference of $RII_{\text{environment}}$ with and without cushions from 0
309 respectively.

310

311 **Results**

312 *Cushions generally increased species richness and abundance*

313 There were significant differences in species richness between cushions and
314 cushion-free areas for all studied 11 sites with 10 communities showing
315 significantly higher species richness in cushions than in cushion-free areas
316 (Fig. 2a). Richness within cushions of *A. polytrichoides* at QES differed little
317 from cushion-free areas but was still significantly lower. With the exception of
318 *A. polytrichoides* at QES, the increase in richness associated with the
319 presence of cushions ranged from c. 5% (*T. caespitosum* at ZGL) to c. 59% (*A.*
320 *lancangensis* at DXS). Differences in richness effects for particular species at
321 different sites ranged from c. 13% in *A. ploytrichoides* (QES vs. BMS) to c.
322 33% in *A. lancangensis* (DDL vs. DXS). In addition, species differences in
323 richness effects within a site were observed for *A. polytrichoides* and *P.*
324 *articulata* in BMS (c. 31%). Eight of the 11 communities (73%) significantly
325 increased mean species abundance, i.e. showing positive $RII_{abundance}$ values
326 (Fig. 2b). There was a marginally significant difference in $RII_{abundance}$ among
327 different studied communities ($F = 1.731$, $P = 0.07$). The proportion of species
328 unique to cushion habitats ranged from 10% (*A. polytrichoides* at QES) to 40%
329 (*A. lancangensis* at DXS) (Table 1).

330

331 *Cushion effects tended to increase with habitat severity*

332 Both ISR ($n = 11$, $r = -0.55$, $P = 0.07$) and $RII_{abundance}$ ($n = 11$, $r = -0.56$, $P =$

333 0.07) showed almost significant correlations with habitat biomass, with
334 facilitation intensity decreasing as habitat biomass increased (Figs. 3a, b).

335

336 *Changes in facilitation intensity with habitat severity due to environmental*
337 *severity and nurse trait effects*

338 Mean $RII_{neighbor}$ showed positive values for low and high severity sites,
339 indicating that there was a significant facilitation effect of the cushions (Fig. 4).

340 Furthermore, $RII_{neighbor}$ in the high severity habitats was significantly higher
341 than $RII_{neighbor}$ at low severity habitats ($n = 3$, $t = -4.722$, $P = 0.042$). Negative

342 values (below zero) of $RII_{environment}$ both with and without cushions indicated
343 higher species richness at the low severity habitat (Fig.4). In addition, both

344 values of $RII_{environment}$, i.e. without ($n = 3$, $t = -5.791$, $P = 0.029$) and with ($n = 3$, t
345 $= -5.920$, $P = 0.029$) cushions, were significantly different from zero indicating

346 the change of facilitation of cushions were due to both environmental severity
347 and nurse trait effects. However, $RII_{environment}$ without neighbor was significantly

348 more negative than with neighbor ($n = 3$, $t = 4.889$, $P = 0.039$), indicating that
349 with increasing environmental severity, species richness in habitats without

350 cushions decreased more strongly than species richness within cushions
351 (Fig.4). Similar patterns were observed for each species separately (Appendix

352 S3).

353

354 **Discussion**

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

364

365 *Environmental context dependence of facilitation*

366 We found an increase of facilitation effects of cushions as habitat severity
367 increased. This provides support for the stress gradient hypothesis (SGH),
368 which proposes that competition should be relatively more frequent in
369 low-stress conditions and facilitation more frequent in high-stress conditions
370 (Bertness & Callaway 1994; Brooker & Callaghan 1998). Even though habitat
371 biomass, our surrogate of environmental severity, is susceptible to other
372 factors than abiotic environmental harshness, in particular to herbivory, with
373 the location of the study sites at the upper altitudinal limit of plants we reduced
374 the impact of such potential confounding factors considerably. All our study
375 sites were characterized by open vegetation suggesting very low grazing
376 intensity (Dorji et al. 2010; 2014).

377 In addition, our study indicated that the change in facilitation of cushion
378 species was driven by an environmental severity effect (i.e. the richness of
379 non-cushion species in cushion-free areas decreased significantly with
380 increasing severity of the habitat). In fact, richness of non-cushion species also
381 decreased in cushions (shown as a negative nurse trait effect) indicating that
382 cushions could not buffer completely the species loss occurring in cushion-free
383 areas. These findings are in accordance with a report in a recent
384 meta-analysis of Michalet et al. (2014), which showed that nurse trait effects in
385 temperate climates mainly acted to increase net competition at low-stress sites
386 while environmental severity effects drove increasing net facilitation at
387 high-stress sites. At one site (BMS), the increased association between
388 non-cushion species and cushions of *A. polytrichoides* towards higher
389 elevations is specifically related to significantly decreased soil nutrient
390 availability with increasing altitude (Yang et al. 2010), therefore corroborating
391 that the buffering effect of cushions likely diminishes with increasing stress,
392 even though net facilitation increases. The net facilitation effect here increases
393 with increasing habitat severity only because the reduction in species richness
394 and abundance is stronger in cushion-free areas compared to cushions. In
395 other words, the increase in facilitation intensity with increasing habitat severity
396 is solely due to an environmental severity effect, but modified in magnitude by
397 the nurse trait effect.

398

399 *Species-specificity of facilitation: a nurse trait effect*

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

421 ecosystem-engineering effects of cushions may be responsible for differences
422 in their facilitation effects.

423

424 *Are nurse trait effects at the basis of deviations from the stress gradient*
425 *hypothesis?*

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

435 Separate studies working with *T. caespitosum* at extremely high elevations
436 (ca. 4800 m - 5900 m) in the Indian Trans-Himalayas (western part of the
437 Tibetan Plateau) with a very cold and dry climate (<100 mm year⁻¹) indeed
438 showed that this exceptionally hard and compact cushion species does not
439 provide microsites with better thermal and nutrient conditions than surrounding
440 open areas, explaining the lack of facilitation of this species (de Bello et al.
441 2011; Dvorský et al. 2013). This suggests the nurse trait effect as the
442 underlying driver of the species-specificity of facilitation observed in our study.

443 Therefore, species-specific nurse trait effects explain the deviations of
444 individual site/species combinations from the general pattern of increasing
445 facilitation with increasing environmental severity. Forthcoming studies in the
446 HHM now need to analysis the interplay between the functional traits of the
447 cushions and the environmental gradients, and their consequences for
448 non-cushion species (Schöb et al. 2013; Michalet et al. 2014).

449

450 **Conclusion**

451 Our results suggest that facilitation by cushion plants is key to structuring
452 diversity and the composition of natural communities at high elevations in the
453 species rich HHM. It is clear now that cushion plants act as 'nurse species' as
454 well as a 'keystone species' in these alpine habitats. Along with a 'real' stress
455 gradient reflected by habitat biomass, the strength of facilitation of cushions
456 increased with increasing habitat severity. Partitioning the net effects of
457 facilitation of cushions showed that the increase of facilitative effects of
458 cushions on species richness with increasing habitat severity appeared to be
459 due to changes in the performance of the response species growing without
460 cushions (i.e. an environmental severity effect). Nurse trait effects, however,
461 modulated the intensity of facilitation. On the one hand, along the severity
462 gradient cushions lost some capacity of environmental buffering, thereby
463 reducing but not eliminating environmental severity effects within the cushion
464 habitat. On the other hand, nurse trait effects were responsible for deviations

465 of some species from the average effect of cushions on diversity. Despite the
466 species-specificity of facilitation by cushion plants in the HHM, their overall
467 positive effect on species diversity indicates that cushion plants may represent
468 efficient biotic refuges for other alpine plants when migrating at higher
469 elevations because of global warming in the HHM. Our results clearly indicate
470 that cushion plants will not lose their facilitative ability for non-cushion species
471 if stress is reduced.

472

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485

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- 648

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

Study sites	Cushion species	Total species	Species unique	Species unique	Shared species
			to cushions (Percentage of total species)	to cushion-free areas (Percentage of total 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

652

653

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

668

669 **Figure 2** a: The number of species estimated by rarefaction curves (mean \pm
670 s.e) within cushions (gray bars) and cushion-free areas (white bars) in each
671 studied community ($n = 20$, the number of replicated rarefaction analyses). $*P$
672 < 0.05 , $**P < 0.01$, $***P < 0.001$. b: Mean relative interaction index
673 ($RII_{abundance}$) (mean \pm s.e) of cushion species in each studied community ($n =$
674 number of non-cushion species). See Fig.1 for abbreviations.

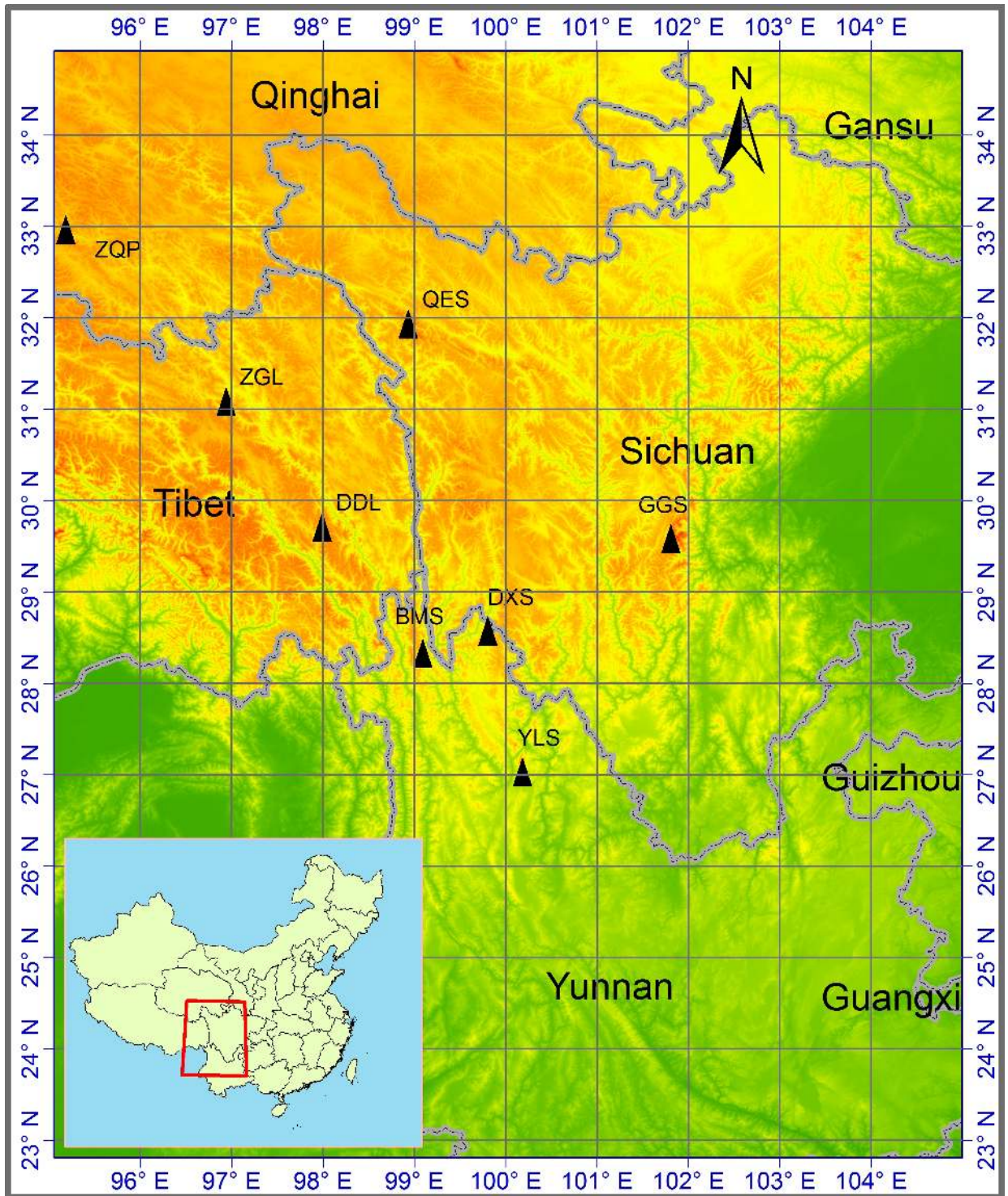
675

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

680

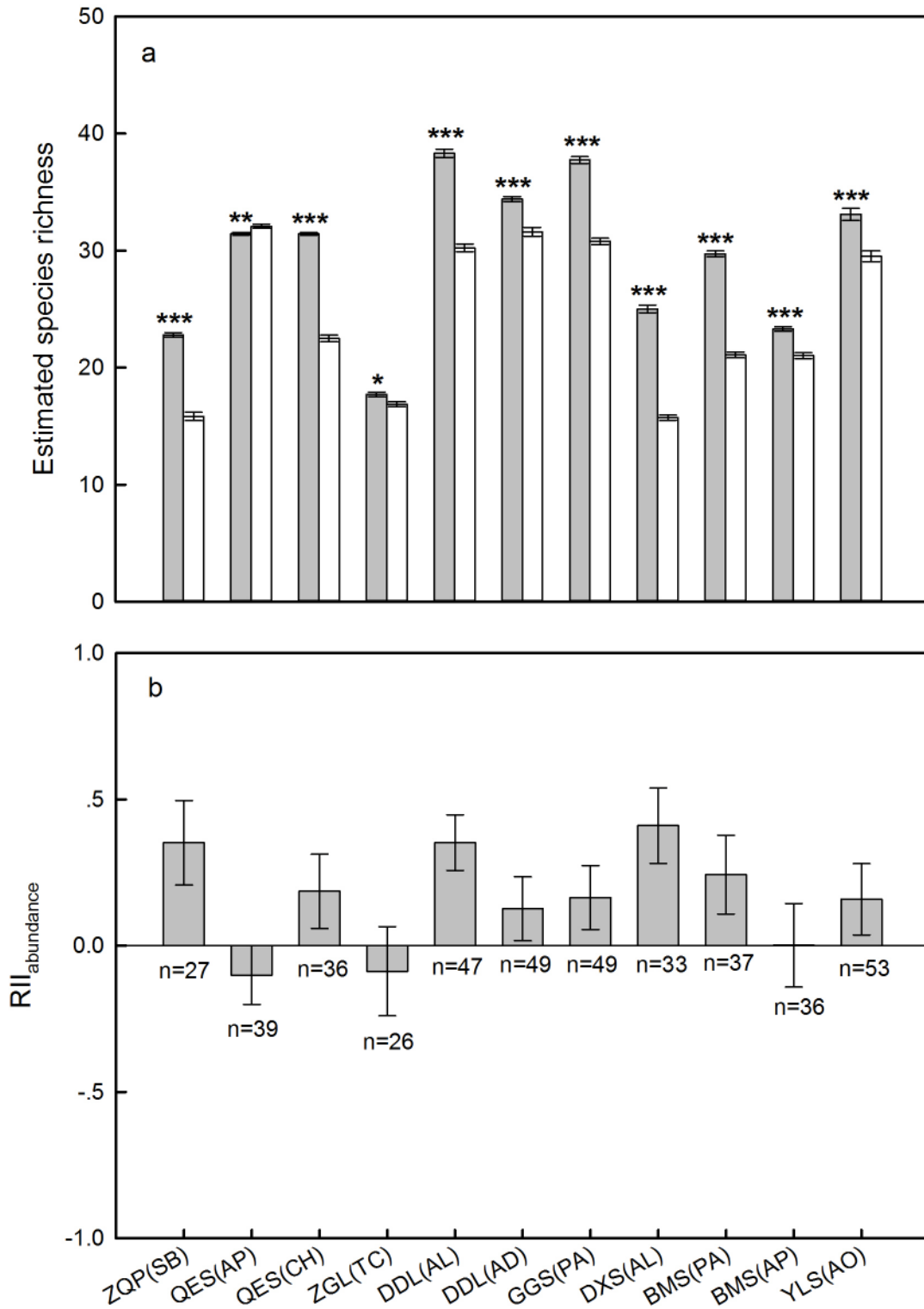
681 **Figure 4** Mean of $RII_{\text{neighbors}}$ at low and high environmental stress (left) and of
682 $RII_{\text{environment}}$ without and with cushions (right) indicating the effect of cushions
683 on species richness at the low and high severity sites and the effect of
684 environmental severity on species richness in cushion-free areas and
685 cushions respectively.

686 Figure 1



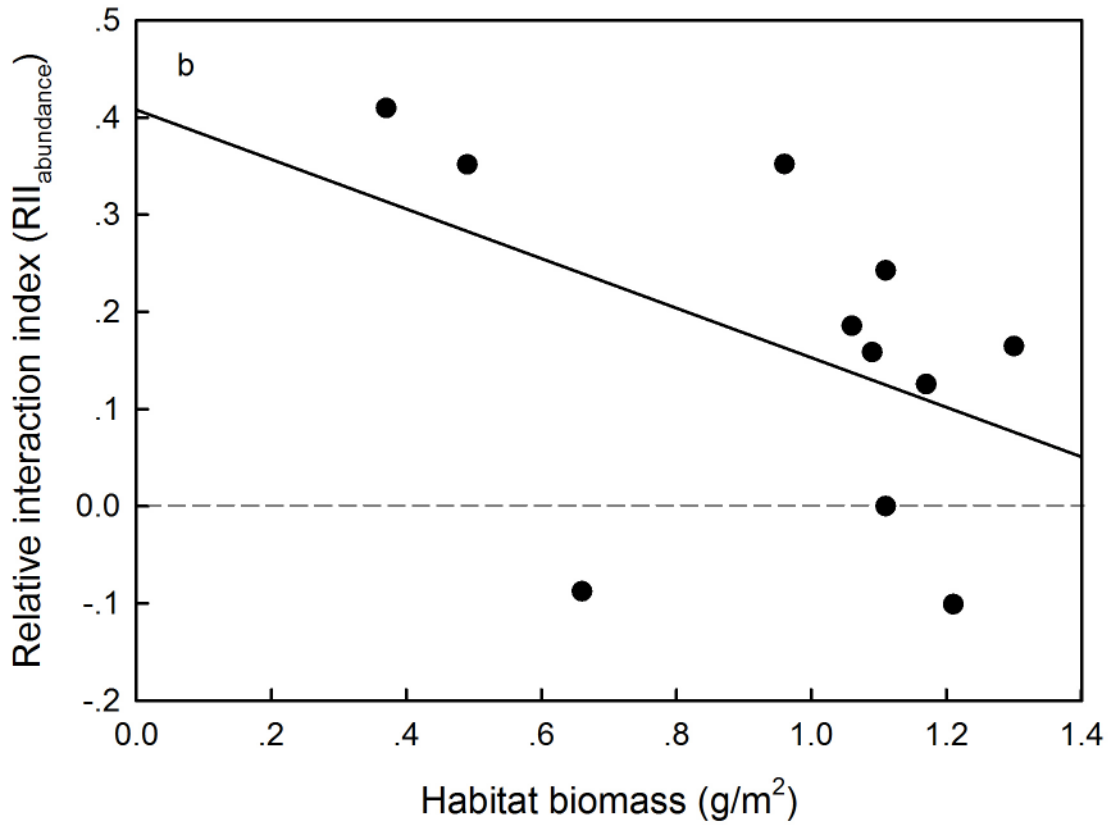
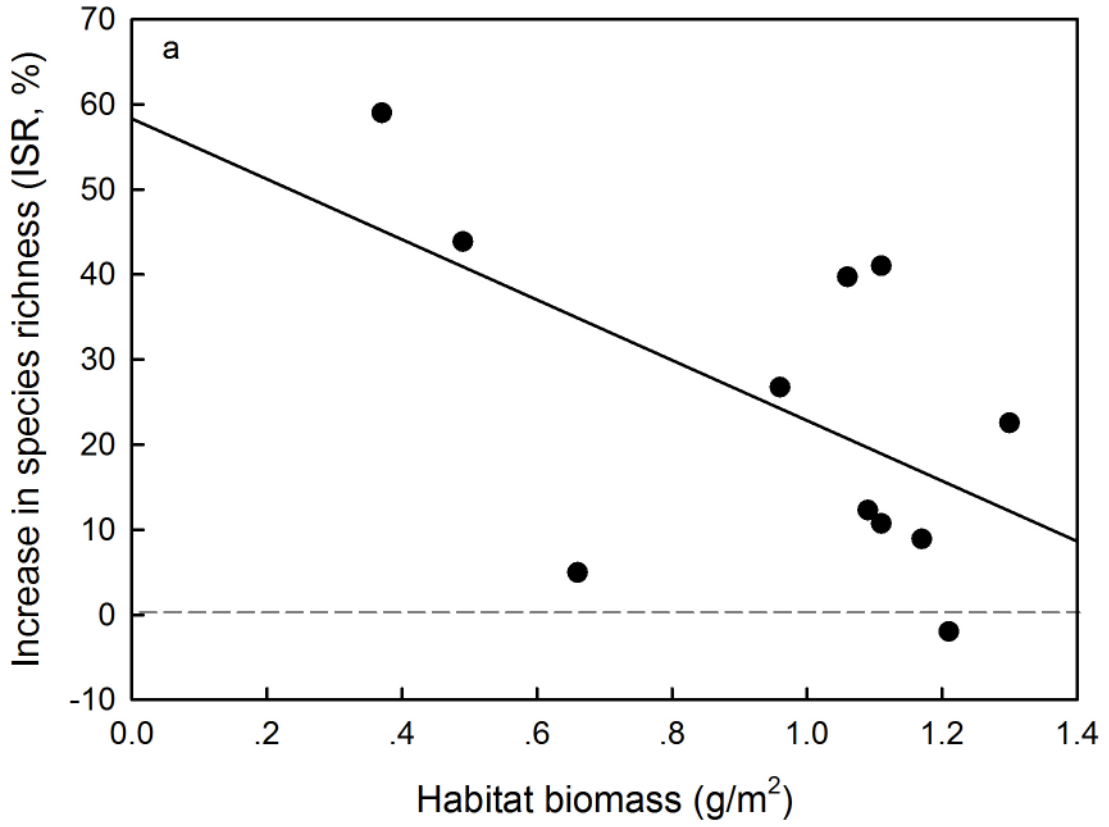
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688 Figure 2



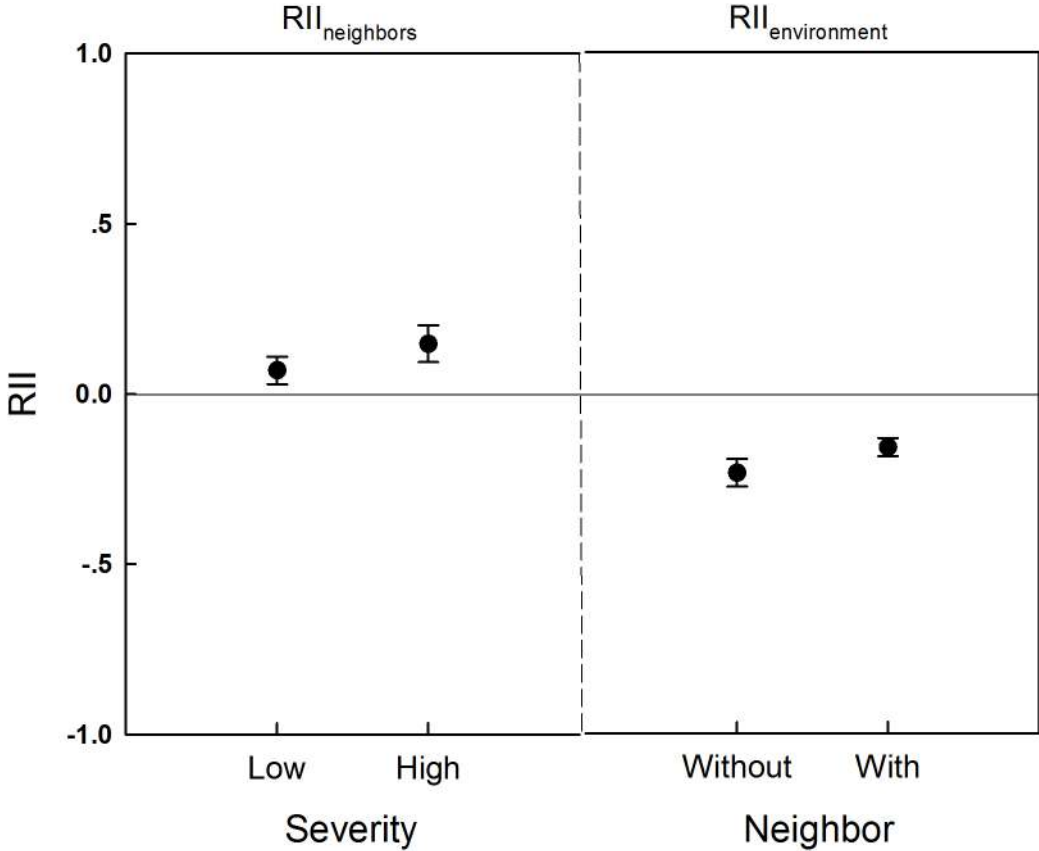
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691 Figure 3



692

693 Figure 4



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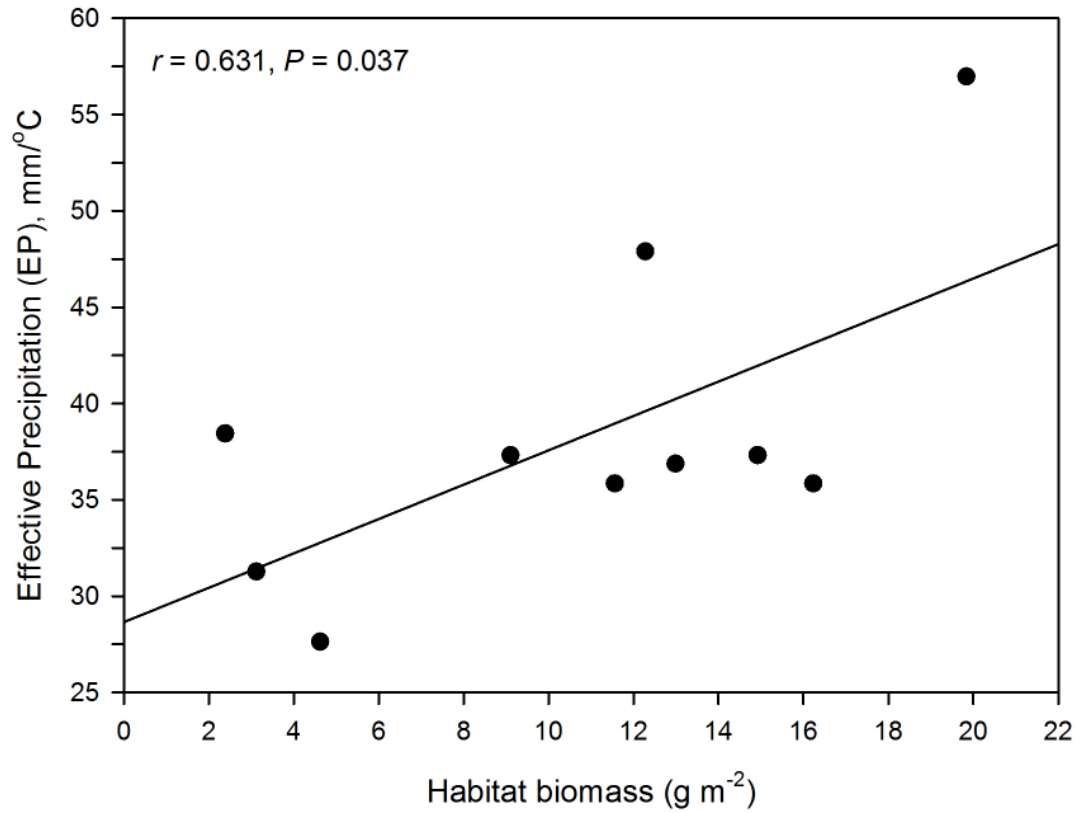
Appendix S1. Details of the 11 communities studied at the upper limit of the plant distribution in the Himalayan-Hengduan Mountains. The table lists the cushion species dominating each plant community, the geographical location (latitude, longitude, elevation), effective precipitation (EP) during growing season (June, July and August) and habitat biomass of each study site, the total number of paired samples (n) taken from cushions and cushion-free areas. EP was calculated for each month and each site as $EP = 12 \cdot P / (T + 10)$, and then averaged over the three months of the growing season. P (monthly precipitation) and T (monthly mean temperature) were obtained from the WorldClim database (<http://www.worldclim.com>) using the geographical coordinates of each site. See Fig.1 for full names of the study sites.

Study sites	Cushion species	Location	Elevation (m)	EP (mm/°C)	Habitat Biomass (g m ⁻²)	n
ZQP	<i>Sibbaldia tetrandra</i>	95°10'59.2"E, 32°57'58.5"N	4800	31.28	3.12	32
QES	<i>Arenaria polytrichoides</i>	98°55'57.1"E, 31°56'11.3"N	5050	35.85	16.23	45
QES	<i>Chionocharis hookeri</i>	98°55'57.0"E, 31°56'11.5"N	5050	35.85	11.56	30
ZGL	<i>Thylacospermum</i>	96°56'13.0"E, 31°05'21.3"N	4400	27.63	4.62	42

caespitosum

DDL	<i>Arenaria lancangensis</i>	97°59'01.7"E, 29°42'43.3"N	5000	37.31	9.10	50
DDL	<i>Arenaria densissima</i>	97°59'01.8"E, 29°42'43.1"N	5000	37.31	14.92	50
GGG	<i>Potentilla articulata</i>	101°48'13.6"E, 29°31'04.9"N	4200	56.97	19.84	35
DXS	<i>Arenaria lancangensis</i>	99°48'22.3"E, 28°34'20.8"N	4500	38.44	2.38	36
BMS	<i>Potentilla articulata</i>	99°05'12.0"E, 28°19'52.5"N	4700	36.88	12.99	50
BMS	<i>Arenaria polytrichoides</i>	99°05'12.0"E, 28°19'52.5"N	4700	36.88	12.99	50
YLS	<i>Arenaria oreophila</i>	100°10'51.05"E, 27°01'57.53"N	4200	47.89	12.28	50

Appendix S2. Relationship between Habitat biomass (g m^{-2}) and Effective Precipitation (EP, $\text{mm}/^{\circ}\text{C}$) during the growing season (June, July and August) of 11 studies sites in the Himalayan-Hengduan Mountains.



Appendix S3. Values of $RII_{\text{neighbors}}$ at low and high environmental stress (left) and of $RII_{\text{environment}}$ with and without cushions (right) for *Arenaria polytrichoides* at QES and BMS (a), *A. lancangensis* at DDL and DXS (b) and *Potentilla articulata* at GGS and BMS (c), respectively. $RII_{\text{neighbors}}$ and $RII_{\text{environment}}$ indicate the effect of cushions on species richness at the low and high severity sites and the effect of environmental severity on species richness in cushions and cushion-free areas respectively.

