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7 **Food and habitat provisions jointly determine competitive and facilitative interactions**
8 **among distantly related herbivores**

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23 **Abstract**

24 1. Interactions between distantly related herbivores exert powerful influences on ecosystems,
25 but most studies to date have only considered unidirectional effects. Few have simultaneously
26 examined the mutual effects that vertebrate herbivores and insect herbivores have on one
27 another.

28 2. We conducted a set of manipulative experiments to evaluate the potential competition and
29 facilitation between two pairs of distantly related herbivore taxa: insect caterpillars
30 (*Gynaephora alpherakii*) and two large vertebrate herbivores, yak (*Bos grunniens*) and Tibetan
31 sheep (*Ovis aries. tibetica*).

32 3. We found that these large herbivores consistently increased the density of caterpillars likely
33 by improving the habitat for caterpillars. The caterpillars, in turn, decreased yak's but
34 increased Tibetan sheep's foraging time and intake bites by differently changing available food
35 resources of the two large herbivores. Diet preferences of herbivores modified the habitat and
36 food resources, thereby causing a diet-mediated competition between yak and caterpillars, and
37 facilitation between sheep and caterpillars. The vertebrate herbivores' non-preference for
38 *Lamiophlomis rotata* and *Gentiana straminea*, the caterpillars' preferred habitat, increased
39 densities of the two plant species, thus favoring the caterpillars. In turn, the caterpillars'
40 preference for *Kobresia pygmaea*, significantly reduced food resources of yak, while promoted
41 food resources (multiple forbs) of sheep.

42 4. *Synthesis*. Our study indicates that two different mechanisms (the changes in habitat and
43 food availability) induced by herbivore jointly determine competitive and facilitative
44 interactions between distantly related herbivore species. We also suggest that examining the

45 bidirectional effects between herbivores offers a better understanding of competition and
46 facilitation in terrestrial animal communities.

47 **Keywords:** Competition, diet preference, facilitation, food availability, forb, habitats,
48 herbivores, *Kobresia pygmaea*

49

50 INTRODUCTION

51 Interactions among herbivores play a central role in maintaining community structure and
52 ecological functioning (Strauss 1991; Kimuyu *et al.* 2017; Koerner *et al.* 2018). However, the
53 vast majority of studies of herbivore-herbivore interactions only consider affects in one
54 direction (Odadi *et al.* 2011; Bakker *et al.* 2013, but see Zhong *et al.* 2014; Dangles *et al.*
55 2018). Facilitation, for example, is usually identified as the positive effect of species A on B,
56 without a concurrent assessment of species B on A. Nevertheless, the interactions between two
57 species should be a ‘bi-directional effect’, and ‘facilitation’ was considered only when
58 encounters between organisms benefit at least one of the participants and cause harm to neither
59 (Bruno *et al.* 2003). Therefore, simultaneously examining the effects of herbivores on each
60 other can give us a clearer understanding of competition vs. facilitation in ecological animal
61 communities.

62 In recent decades, interspecific interactions among distantly related herbivores have been
63 increasingly identified, and both competition (Denno *et al.* 1995; Ohgushi 2005; Wilkerson *et*
64 *al.* 2013) and facilitation (Kuijper *et al.* 2008; Bakker *et al.* 2009) have been found. However,
65 the majority of such studies have classically investigated the effects of large herbivores on
66 smaller ones (Enans *et al.* 2006; Pringle 2007; Poelman *et al.* 2008). For example, large

67 mammalian herbivores depress small rodents or invertebrate herbivores that rely on host plants
68 in the Africa savanna (Keesing 1998), an alpine meadow (Steen *et al.* 2005), and a coastal
69 dune community (Huntzinger & Lawton 2008). Additionally, larger herbivores successively
70 facilitate smaller herbivores by improving or stimulating growth of higher quality forage
71 (Gordon 1988). Since the concept of ‘indirect interaction webs’ was presented (Ohgushi 2005),
72 ecologists found that small herbivores such as herbivorous insects are an overlooked, but
73 potentially important factor that indirectly influenced the foraging behavior of large herbivores.
74 For example, a species of caterpillar increased a pika’s actively selected areas (Barrio *et al.*
75 2013), and grasshoppers benefitted sheep’s foraging time during the peak of vegetation
76 growing season (Zhong *et al.* 2014). Despite these suggestive results, the mechanisms to
77 answer how small herbivores alter large herbivore performance, especially how insect
78 herbivores affect mammalian herbivores, remains fragmentary at best.

79 Herbivores may interact with each other via a variety of mechanisms, and they may engage
80 in some combination of competition or facilitation when they both share the same plant
81 resources or occupy the same space. Experimental investigations across different habitats have
82 revealed that herbivores affect each other mainly by two key aspects: trophic resource
83 availability (McNaughton 1976; Murray & Illius 2000) and habitat structure (Torre *et al.* 2008;
84 Woodcock & Pywell 2009; Sendoya & Oliveira 2015). One herbivore species can induce plant
85 compensatory growth by foraging and cause changes in the quantity or quality of its host plant,
86 thus having important consequences for another herbivore species using the same host
87 (McNaughton 1983; Odadi *et al.* 2011). Some herbivore species can act as ‘ecosystem
88 engineers’ through their foraging, trampling, burrowing activities (Jones *et al.* 1997), and

89 strongly modify the habitat structure for other species (Davidson *et al.* 2007; Bakker *et al.*
90 2009). Some larger herbivorous insects like leaf-rolling caterpillars benefit small aphids by
91 providing utilizing leaf shelters (Nakamura & Ohgushi 2003). Additionally, herbivores can
92 interact with each other through sharing the same natural enemies, which could increase or
93 decrease the predation risk (Holt & Lawton 1994; Schmitz 2008). Moreover, herbivores may
94 affect each other by direct means (Gish *et al.* 2017; Berman *et al.* 2017). For example, in the
95 semi-natural grasslands of the Netherlands, high grazing intensity of sheep increased the nest
96 damage and mortality of the caterpillars by incidental ingestion (van Noordwijk *et al.* 2012).

97 The Qinghai-Tibetan plateau, known as ‘the third pole’ in the world, extends 2.5 million
98 km², approximately 25% of the area of China, and provides a unique environment for a wide
99 variety of alpine flora and fauna. Alpine meadow, covering about 35% of the plateau, is the
100 representative vegetation and main pastureland in the area (Cao *et al.* 2015). The generalist
101 caterpillars of the tussock moth *Gynaephora alpherkii*, yak *Bos grunniens*, and Tibetan sheep
102 *Ovis aries. tibetica* are the most important herbivores that have coexisted for thousands of
103 years. These herbivores play a vital role in maintaining community structure and ecological
104 functioning of alpine meadow grassland (Cao *et al.* 2015). Nevertheless, the interactions
105 among those herbivores remain unstudied.

106 Here, we conduct a set of manipulative field experiments to examine the simultaneous
107 effects among two large vertebrate herbivores (yak and Tibetan sheep) and an insect herbivore
108 (caterpillars) with different diet preferences to evaluate the competitive or facilitative
109 interactions among them. Previous works have shown that caterpillars and yak prefer to
110 consume the dominant sedge *Kobresia pygmaea* (Wan & Zhang 2006; Ding *et al.* 2006), we

111 therefore hypothesized that caterpillars and yak exert a competitive interaction because of food
112 competition between them. In contrast, Tibetan sheep prefer forbs (Ding *et al.* 2006).
113 Caterpillars' preference for dominant sedge *K. pygmaea* might reduce the competition to forbs,
114 thus increase biomass of forbs and thereby facilitate Tibetan sheep's foraging for preferred
115 forbs. Similarly, sheep's preference for forbs might further facilitate Caterpillars' foraging for
116 *K. pygmaea* due to release of completion. We therefore hypothesized that caterpillars and
117 Tibetan sheep exert a facilitative interaction. Additionally, the caterpillars prefer to live in two
118 broad-leaf forbs, *Lamiophlomis rotata* and *Gentiana straminea* (D. Pan & X. Li, *personal*
119 *observations*, Supplementary, Fig. S1), which were never eaten by yak or Tibetan sheep
120 (Supplementary, Table. S1). Therefore, grazing by yak and Tibetan sheep might release the
121 completion of the two broad-leaf forbs, which could increase their densities and potentially
122 improve habitat for caterpillars. We tested these hypotheses by measuring consumer and
123 vegetation responses to various combinations of herbivores, and then discuss the underlying
124 mechanisms related to habitat and food resources availability based on herbivore diets.

125

126

127 **MATERIALS AND METHODS**

128 ***Study site and background***

129 We conducted our research at the Alpine Grassland Ecological Research Station of Tsinghua
130 University-Qinghai University located in Qinghai-Tibetan plateau (33°20' N, 97°25' E, 4290
131 m above sea level), Qinghai Province, China for 2 years. This study site has a continental
132 alpine climate, with severe and long winters and short cool summers. The annual mean

133 temperature is around -4.4°C (ranging from -13.3°C in January to 9.2°C in July), and annual
134 mean precipitation is about 430 mm, with 70% falling in June-August. The soil is classified
135 as Mat Cry-gelic Cambisols (Cao *et al.* 2004).

136 The native grassland at the study site was dominated by the perennial sedge *K. pygmaea*. Other
137 major species included sedges such as *Kobresia tibetica*, *Kobresia humilis* and *Carex*
138 *scabrostris*, grasses such as *Stipa aliena*, *Poa patensis* and *Elymus nutans*, and forbs such as
139 *Aster flaccidus*, *Potentilla discolor*, and *Saussure stella*. The broad-leaf forbs, *L. rotata* and *G.*
140 *straminea*, were evenly distributed across the grassland. The site has been supporting
141 pastoralism of domesticated yak *B. grunniens*, Tibetan sheep *O. aries* and Tibetan horse *Equus*
142 *caballus tibetica* for several thousand years, and yak and Tibetan sheep are the two main
143 domestic herbivores. The caterpillar, *G. alpherakii*, is the most important herbivore insect and
144 was abundant during all years at the study site (Fig S1). Caterpillar eggs hatch in late summer
145 and early fall and overwinter as first instars. Caterpillars grow quickly from late spring to
146 middle summer (early May to middle August) and are highly visible. They pupate,
147 metamorphose into tussock moths, and reproduce in late summer (Yan *et al.* 2006).

148 ***Experimental design and management***

149 We established a manipulative field grazing experiment in the study site in 2013. The
150 experiment employed a randomized block design and consisted of nine plots with similar
151 vegetation characteristics and initial caterpillars densities arranged in three blocks of three
152 (measured before the experiment, see Table S2). The blocks were parallel to each other, with
153 a distance of 50 m from neighboring blocks. Each plot was 100×100 m in size and fenced
154 with barbed wire. Neighboring plots within blocks were separated by 30 m (see Fig. S2). Each

155 plot within a block was randomly assigned to receive one of the following treatments: yak
156 grazed, Tibetan sheep grazed, and vertebrates excluded (control). Grazing was maintained at
157 a moderate intensity in each herbivore treatment (approximate 50% of aboveground plant
158 biomass removal during the growing season; stocking rate was about 6.17 sheep ha⁻¹). The
159 manipulated grazing season was similar to the season for free grazing in this region: from the
160 second week of June through the last week of September. Grazing activity lasted for 12 hours
161 (from 06:00 h to 18:00 h) on each day.

162 In May 2013, we designated four pairs of 5 × 5 m subplots on each plot (a total of 36 pairs
163 of subplots at the study site). Each pair of subplots consisted of a randomly-selected
164 caterpillars' present and a caterpillars' absent treatment (see Fig. S2). The caterpillars' absent
165 subplots were hand-sprayed twice a week or after heavy rains with a commercially available
166 imidacloprid pesticide (10 ppb imidacloprid solution, 10 ml of solution diluted in 1 L water)
167 which was effectively against caterpillars (see Table. S3 and Table. S4) and widely used for
168 decades in this region. Additionally, the imidacloprid had no effect on the growth of plant (see
169 Table. S5). The caterpillars' present subplots were also hand-sprayed only with water at the
170 same time with caterpillars' absent subplots. Inspections were made between insecticide
171 treatments on the exclusion plots, and any caterpillars observed on these plots were removed.
172 The caterpillars' exclusion manipulation was from the third week of May through the second
173 week of August. The manipulation was repeated in 2014.

174 *Diet selection of large herbivores (yak and Tibetan sheep) and caterpillars*

175 In August 2014, we measured the diet selection of large herbivores at the plot scale. Four 40-
176 m linear transects were laid out in each grazed plot (except in the four pairs of 5 × 5 m subplots),

177 and ten 0.5×0.5 m quadrats spaced 4 meters apart were placed along each transect. We
178 measured the percentage of plant species (P) of each transect. We recorded and assigned with
179 a value of one for each plant species in the quarter, and then summed the values of each species
180 per transect (each recorded species of the transect obtained a value from 1 to 10, marked with
181 'V'). The percentage of each species among all recorded species in the transect was calculated
182 by the following equation: $P = V_i / \sum_{i=1}^n V_i$, where V_i is the summed value of the species i in
183 the transect, and n is the number of all recorded species in the transect. Additionally, we
184 measured the grazing frequency (GF) of each plant species fed by the herd in the transect. We
185 recorded species fed by the animals by indirect observations (direct observations were not
186 possible because yak and Tibetan sheep did not allow close approach). We waited until the
187 herd had fed and moved away from the quarter, and then visited the quarter and recorded the
188 eaten species from the feeding signs (Mishra *et al.* 2004). This allowed identification of plant
189 species fed upon by the animals (Supplementary: Fig. S3). We assigned with a value of one
190 for grazed plant species, and zero for untouched species in the quarter. We summed the values
191 of each plant species per transect (each plant species in the transect obtained a value from 0 to
192 10, marked with 'GV'). The grazing frequency of each plant species in the transect was
193 calculated by the following equation: $GF = GV_i / \sum_{i=1}^n GV_i$, where GV_i is the summed value of
194 the species i in the transect, and n is the number of species recorded in the transect. We used
195 selectivity index (SI) to describe diet preference of yak and Tibetan sheep. SI was calculated
196 based on the following equation: $SI = GF / P$. The average SI for the four transects in each plot
197 was then used in analyses.

198 On a sunny day in early August 2014, we investigated the diet selection of caterpillars.

199 Firstly, the percentage of plant species (P) in each ungrazed plot were measured by using the
200 same method with grazed plot (see above). We then investigated the percentage of feeding
201 time (PFT) of the species fed by caterpillars. We randomly chose nine caterpillars from
202 ungrazed plots (three caterpillars in each plot) and installed an identifying red paint mark on
203 their backsides and abdomens to facilitate observation. We recorded the caterpillars' feeding
204 time on different plant species, and all individuals were observed for eight hours continuously
205 from 09:00 to 17:00. The percentage of feeding time (PFT) of the species fed by caterpillars
206 was calculated using the following equation: $PFT = FT_i / \sum_{i=1}^n FT_i$, where FT_i is the total
207 feeding time of the plant species i for the observation period, and n is the number of species
208 fed by caterpillars. The selectivity index (SI) was calculated based on the following equation:
209 $SI = PFT / P$. We used the average SI for the three caterpillars in each plot for the analyses.

210

211 *Effects of large herbivores on caterpillars' density*

212 From 5 June to 11 August 2014, we surveyed caterpillars' density weekly both in large-
213 herbivore-grazed and ungrazed plots (total of 11 times during the experiment). Two 100 m
214 lines between the plot corners were placed in each plot, and six 1×1 m quadrats were evenly
215 placed along each diagonal line. We walked along each transect and counted the number of
216 caterpillars in each quadrat, and then calculated the average density across the two transects
217 in each plot. The sum of the 11 counts in each plot was used for the analyses.

218

219 *Effects of large herbivores on main food resources and habitat of caterpillars*

220 In mid-August 2014, we measured the biomass of the dominant species *K. pygmaea* in twelve

221 0.5 × 0.5 m quadrats along the two diagonal lines in each plot. We clipped, dried, and weighted
222 the plants at 60°C for 48 h to estimate plant biomass per square meter.

223 In late August 2014, we randomly placed five 5 × 5 m quadrats in each plot (except in the
224 four pairs of 5 × 5 m subplots), and counted the number of *L. rotata* and *G. straminea* plants
225 in each quadrat. The five samples were then used to estimate the density for the two species
226 per square meter.

227

228 ***Effects of caterpillars on the foraging behavior and food resources of large herbivores***

229 In early August 2014, we measured the foraging time (total seconds within the hour that the
230 herbivores feed) and intake bites (bites within the hour that the herbivores feed) by yak and
231 Tibetan sheep in each subplot in the large-herbivore grazed plots. The observations of large
232 herbivore foraging behaviors were conducted twice daily (08:00 to 10:00 in the morning and
233 15:00 to 17:00 in the afternoon), for a total of four hours each day. The observations lasted for
234 three days. The total foraging time and intake bites for a continuous two hours observation
235 were recorded.

236 In mid-August 2014, we measured the biomass of *K. pygmaea* and forbs including *A.*
237 *flaccidus*, *P. discolor* and *S. stella* by randomly selecting three 0.5 × 0.5 m quadrats in each
238 subplot. The sampling methods were the same as described above.

239

240 ***Statistical analyses***

241 All analyses were performed with software R version 3.5.3 (R Core Team 2019). We used
242 linear mixed effect models (LMMs) from the lme4 package (Bates *et al* 2015) to test the effects

243 of grazing on caterpillars and plants. Biomass of *K. pygmaea*, density of *L. rotata* and *G.*
244 *straminea* were included as response variables separately. Grazing treatment (three levels:
245 control, sheep and yak) was included as a fixed factor, block and nested sampling replicates
246 as random factors. Tukey tests between treatments comparisons were performed by multcomp
247 package (Hothorn *et al* 2008) after each LMM. For dynamics of caterpillars (density in weekly
248 sampling time), we performed a repeated measures LMM (with grazing treatment, sampling
249 time and their interaction as fixed factors; plot ID of each treatment within block (e.g. ‘block1-
250 yak’) and sampling time as random effects, where time was also treated as a temporal
251 autocorrelation structure of order one-corAR1 in the model). To test the relationship between
252 caterpillars and the broad-leaf forbs, we used a simple linear model to regress the total
253 caterpillars’ density against the density of plant species including *L. rotata* and *G. straminea*
254 separately by all plot-scale samplings in the site. To test the impacts of caterpillars on plants
255 (including biomass of *K. pygmaea* and forbs comprising *A. flaccidus*, *P. sibiricum*, and *S. stella*)
256 within each grazing treatment plots separately, we used LMMs with caterpillars treatment (two
257 levels: removed and control) as a fixed effect while block and paired subplots as random
258 effects. To test the impacts of caterpillars on large-herbivore foraging behaviors (including
259 intake bites and foraging time), we used LMMs with caterpillars treatment as a fixed effect
260 while block, paired subplots and also large herbivore individual (considering the possible
261 foraging variation between individuals) as random effects For all models, residual plots were
262 visually inspected to ensure no obvious deviations from homoscedasticity or normality. If not,
263 response variables were transformed by log or square root to meet the model assumptions.

264

265

266 **RESULTS**

267 ***Diet selection of large herbivores and caterpillars***

268 Diet selection of yak and Tibetan sheep differed substantially in our study site (Fig. 1A). Yak
269 particularly preferred the dominant species *K. pygmaea* (SI: 1.27 ± 0.14), followed by *S. aliena*,
270 *P. discolor*, *S. stella*, and *A. flaccidus* (SI: 0.75 ± 0.11 , 0.60 ± 0.04 , 0.52 ± 0.04 , and $0.47 \pm$
271 0.04 , respectively). In contrast, Tibetan sheep preferred the forbs, *A. flaccidus*, *P. discolor* and
272 *S. stella* (SI: 1.47 ± 0.06 , 1.37 ± 0.06 , and 1.21 ± 0.11 , respectively). Caterpillars
273 predominantly consumed *K. pygmaea* (SI: 1.44 ± 0.11 ; Fig. 1B).

274

275 ***Effects of large herbivores on caterpillars' density***

276 The density of caterpillars was significantly affected by the large herbivores ($F = 717.69$, $df =$
277 $2, 13$, $P < 0.001$), and time ($F = 17.39$, $df = 1, 85$, $P < 0.001$), but not affected by time \times large
278 herbivore interaction ($F = 0.56$, $df = 2, 85$, $P = 0.574$). Large herbivore plots had significantly
279 higher caterpillar densities compared with ungrazed plots (Fig. 2A). The total density of
280 caterpillars was 35% and 21% higher in yak and Tibetan sheep grazed plots, respectively, than
281 the control. Caterpillars' densities showed a clear pattern over time, and generally increased
282 from 5 June and to a peak level in 10 July and then sharply declined by 11 August (Fig. 2B).

283 ***Effects of large herbivores on main food resources and habitat of caterpillars***

284 Yak and Tibetan sheep had significant effects on aboveground biomass of food resources, *K.*
285 *pygmaea*, for the caterpillars (Fig. 3A). The biomass of *K. pygmaea* was consistently lower on
286 grazed plots than ungrazed plots in August 2014 ($F = 115.99$, $df = 2, 60$, $P < 0.001$; Fig. 3A).

287 The biomass of *K. pygmaea* on yak and sheep grazed plots were only 27% and 53% compared
288 with the control. Additionally, yak grazed plots had significant lower biomass of *K. pygmaea*
289 than sheep grazed plots.

290 Yak and sheep grazing significantly increased the densities of *L. rotata* and *G. straminea*.
291 The densities of *L. rotata* and *G. straminea* were higher on the yak grazed plots than Tibetan
292 sheep grazed plots ($F = 46.02$, $df = 2, 4$, $P = 0.0017$, for *L. rotata*; $F = 45.49$, $df = 2, 4$, $P =$
293 0.0018 , for *G. straminea*; Fig. 3B, C). The densities of *L. rotata* and *G. straminea* were 97%
294 and 80% higher in yak grazed plots respectively than the control, and 67% and 32% higher in
295 sheep grazed plots respectively than the control.

296

297

298 ***Relationships of caterpillars with L. rotata and G. straminea***

299 Regression analysis revealed that the density of caterpillars was positively related to the
300 density of *L. rotata* ($r^2 = 0.90$, $F = 64.44$, $df = 1, 5$, $P < 0.001$; Fig. 4A) and *G. straminea* (r^2
301 $= 0.87$, $F = 47.68$, $df = 1, 5$, $P = 0.001$; Fig. 4B) in the nine plots.

302

303 ***Effects of caterpillars on the foraging behavior of larger herbivores***

304 Caterpillars had opposite effects on the foraging behavior of yak and sheep (Fig. 5). The
305 foraging time and intake bites of yak significantly decreased in the subplots in the presence of
306 caterpillars (foraging time: $F = 6.70$, $df = 1, 23$, $P = 0.016$; Fig. 5A; intake bites: $F = 6.92$, df
307 $= 1, 23$, $P = 0.015$; Fig. 5B). The foraging time and intake bites of yak were 18% and 20%
308 lower in caterpillar-present subplots respectively than caterpillar-absent subplots. In contrast,

309 Tibetan sheep had significant higher foraging time and intake bites in the subplots where
310 caterpillars remained (foraging time: $F = 18.75$, $df = 1, 23$, $P < 0.001$; Fig. 5A; intake bites: F
311 $= 14.97$, $df = 1, 23$, $P < 0.001$; Fig. 5B). The foraging time and intake bites of sheep were 22%
312 and 20% higher in caterpillars' present subplots respectively than caterpillar-' absent subplots.

313

314 *Effects of caterpillars on available food resources of large herbivores*

315 Caterpillars had significant but opposite effects on the biomass of *K. pygmaea* and forbs (Fig.
316 6). The biomass of *K. pygmaea* was significantly lower when caterpillars were present in the
317 subplots of the all plots ($F = 25.12$, $df = 1, 11$, $P < 0.001$; Fig. 6A). The biomass of *K. pygmaea*
318 in caterpillar-present subplots was 70%, 73%, and 80% respectively in yak grazed plots, sheep
319 grazed plots and controls than those in caterpillar-absent subplots. In contrast, the biomass of
320 forbs *A. flaccidus*, *P. sibiricum*, and *S. stella* was higher in subplots when caterpillars were
321 present ($F = 200.69$, $df = 1, 11$, $P < 0.001$; Fig. 6B). The biomass of forbs in caterpillar-present
322 subplots increased by 25%, 34%, and 56% in yak grazed plots, sheep grazed plots and controls,
323 respectively, relative to those in caterpillar-absent subplots.

324

325 **DISCUSSION**

326 Our results suggest that the caterpillars exerted a positive interaction with Tibetan sheep and
327 a negative interaction with yak, and demonstrate the bi-directional effects between distantly
328 related herbivore species in our system. Most previous studies on potential interactions
329 between distantly related herbivores have examined the effects of vertebrate herbivores on
330 insect herbivores, and announced a facilitation or competition based on the outcome (see

331 Introduction). In this study, both yak and Tibetan sheep had a positive effect on the density of
332 caterpillars (Fig. 2), which traditionally would be identified as a facilitation interaction
333 between the vertebrate and invertebrate herbivores if only the effect in one direction was
334 considered. However, we found that caterpillars posed a significant positive effect on Tibetan
335 sheep while a negative effect on yak due to diet differences between yak and sheep (Fig. 5).
336 Caterpillars and sheep demonstrated a two-way facilitation, while caterpillars and yak
337 demonstrated facilitation for the insect and competition towards the mammal. Our study
338 therefore provides evidences of the complexity of interactions between distantly related
339 herbivores by testing bi-directional effects in terrestrial animal communities.

340 Our study further showed that diet preference of herbivores determined the competitive or
341 facilitative interactions between distantly related herbivores. Moreover, the interactions
342 between vertebrate herbivores and insect herbivore were driven mainly by two different
343 mechanisms. Large herbivores affect the insect herbivore by modifying habitat, while insect
344 herbivore affect large herbivores by changing the available food quantity.

345

346 ***Effects of vertebrate herbivores on insect herbivores***

347 The positive effects of large herbivores-yak and sheep on insect herbivore -caterpillars in this
348 study, was a result of the increased food availability or habitat modification. However, we
349 found that yak grazing significantly reduced the biomass of *K. pygmaea* as predicted due to
350 its high preference for *K. pygmaea* (Fig. 1). Furthermore, Tibetan sheep grazing also reduced
351 the biomass of *K. pygmaea* (Fig. 3A). The large herbivore foraging-induced reduction in
352 biomass of *K. pygmaea*, the most important food source for caterpillars, therefore could

353 negatively affect density of caterpillars due to reduced food availability. Thus, the altered food
354 resources for the caterpillars cannot explain the indirect positive effects of large herbivores on
355 caterpillars. In our study system, *L. rotata* and *G. straminea* are the main shelter habitat for
356 caterpillars. As predicted, both yak and Tibetan sheep grazing significantly increased the
357 densities of the two broadleaf forbs, which could positively affect density of caterpillars (Fig.
358 3B, C). We also found that the densities of the two plant species were significantly and
359 positively related to that of the caterpillars (Fig. 4). Therefore, relative to available food
360 resources, habitat could be more important in mediating the net effects of large vertebrate
361 herbivores on insect herbivores. Previous studies also found that large herbivores pose great
362 impacts on habitat structure of smaller species through feeding or trampling activities (Frago
363 *et al.* 2012; Berman *et al.* 2018).

364 There are also some other potential mechanisms that could be important to explain the
365 impacts of large herbivores on the smaller species. For example, Large herbivores may change
366 the chemical composition of food plant, such as induced secondary growth on their host plant,
367 improving nutrient quality, which could be benefit small herbivores sharing the same plant
368 (Bakker *et al.* 2009). Large herbivores may also facilitate insect herbivores by breaking down
369 the associational plant defenses, making the host plant more susceptible to insect herbivores
370 (Zhong *et al.* 2014), and by reducing the abundance of predators (Schmitz 2008). These
371 hypothetical mechanisms are beyond the scope of our present study, although further
372 experiments are underway to evaluate these multiple indirect effects. Studies exist
373 demonstrating negative effects of larger herbivores on smaller ones (Takagi & Miyashita 2014;
374 Foster *et al.* 2014), and our results indicated that the facilitation between distant related

375 herbivores might be prevalent in the animal community.

376 .

377 ***Effects of insects herbivores on vertebrate herbivores***

378 The effects of insects herbivores on larger herbivores have received less attention, and usually
379 reported when the herbivorous insects constitute a pest (Musser *et al.* 2002; Berman *et al.*
380 2017). An early study showed that caterpillars increased pika's foraging activity in Canada
381 alpine tundra (Barrio *et al.* 2013), and grasshoppers benefited sheep's access to palatable forbs
382 in the eastern region of the Eurasian Steppe Zone (Zhong *et al.* 2014), but the underlying
383 mechanisms remained unexplored or limited. With the exception of insect outbreaks,
384 herbivorous insects are deemed to typically consume a small fraction of the available plant
385 foliage and thus have little impact on plant population dynamics (Crawley 1989). Also, the
386 biomass removal by herbivorous insects is likely to be non-significant relative to large
387 herbivores (Demment & van Soest 1985; Illius & Gordon 1992). However, there is a growing
388 evidence indicating that small herbivores such as insects can alter competition abilities of
389 plants and primary productivity at a local scale (Rees & Brown 1992; Schädler *et al.* 2007;
390 Kim *et al.* 2013; Loïc *et al.* 2018), and they rapidly influence the vegetation characteristics when
391 their densities are relative high (Zhang *et al.* 2011). In our study site, the total density of
392 caterpillars during the experiment period was very high (exceeded 250 no. /m², Fig. 2A). As
393 expected, the caterpillars reduced the biomass of the dominant species, *K. pygmaea* (Fig. 6A),
394 the main food resource for yak and caterpillars, thus negatively affecting yak foraging.
395 Nevertheless, caterpillars' preference for *K. pygmaea* increased the biomass of forb species *A.*
396 *flaccidus*, *P. sibiricum* and *S. stella*, as the main food for Tibetan sheep, thereby increasing the

397 available food resources for sheep. Therefore, in this study the caterpillars indirectly facilitated
398 sheep grazing and competed with yak by distinctively changing available food quantity for
399 large herbivores-yak and sheep. However, we are not sure whether insect herbivory could
400 change the chemical composition of food plants, such as altering nutritive value, and thus
401 affecting other herbivores.

402 In alpine meadow grasslands of Qinghai-Tibetan Plateau, grassland degradation has
403 increasingly become a serious problem. Our results suggest that the effects of small
404 herbivorous insects on large herbivores should receive more attention in these degraded
405 grassland ecosystems. Furthermore, the observed patterns may be more complex when more
406 herbivore species are included, e.g., the common small mammal lagomorphs of high-altitude
407 grasslands, the Plateau pika (*Ochotona curzoniae*). Future research should comprehensively
408 investigate the interactions among multiple herbivores including this small burrowing
409 mammal.

410

411 **CONCLUSIONS**

412 Testing the bi-directional effects between herbivores is necessary to understand the structure
413 of herbivore assemblages and the facilitative or competitive interactions between them.
414 Distantly related herbivores affect each other in different ways: large herbivores affect small
415 herbivore insects mainly through modifying habitat structure and small herbivore insects affect
416 larger herbivores by changing their food quantity (Fig. 7). Our study indicates that interactions
417 between distantly related herbivorous species in terrestrial animal communities are complex
418 and that animal diet preference is viewed as a good predictor for the facilitative or competitive

419 interaction between distantly related herbivores. Clearly, examining the effects of herbivores
420 on each other simultaneously is essential to our understanding of competition and facilitation
421 in terrestrial animal communities.

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428

429 **AUTHOR CONTRIBUTIONS**

430 D.F.P. and X.C.L. contributed equally to this work. L.W., D.L.W., and D.F.P. designed the
431 research and wrote the draft manuscripts. D.F.P., X.C.L., K.J.D. and C.G. performed the
432 research and analyzed data. G.Q.F. and T.R.S. commented on draft manuscripts. Z.W.Z. and
433 H.Z. developed the figures. S.Z.B. contributed to data collection. All authors edited the
434 manuscript.

435

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652

653

654 **Figure legends**

655 **Fig. 1.** Selective index of the main plant species foraged by yak, sheep and caterpillars.

656 **Fig. 2.** Density of caterpillars. (A) Total density in different herbivore-grazed plots. (B) The
657 dynamic of caterpillars' density in different herbivore-grazed plots during the study period.
658 Different letters above the bars indicate significant difference at $P < 0.05$. Error bars represent
659 \pm SE.

660 **Fig. 3.** Effects of large herbivores on the main food resources and habitat of caterpillars.

661 Biomass of *K. pygmaea* (A), density of *L. rotata* (B), and density *G. straminea* (C). Different
662 letters above the bars indicate significant difference at $P < 0.05$. Error bars represent \pm SE.

663 **Fig. 4.** Relationship between density of caterpillars and (A) *L. rotata* and (B) *G. straminea* in
664 the nine plots (six grazed and three ungrazed plots).

665 **Fig. 5.** Foraging behavior of large herbivores in caterpillar-absent and present subplots. (A)
666 Total intake bites. (B) Total foraging time. Different letters above the bars indicate significant
667 difference at $P < 0.05$. Error bars represent \pm SE.

668 **Fig. 6.** Food resources of large herbivores in caterpillarabsent and present subplots.
669 Aboveground biomass of (A) *K. pygmaea* and (B) forbs *A. flaccidus*, *P. sibiricum*, and *S. stella*.
670 Different letters above the bars indicate significant difference at $P < 0.05$ within each large
671 herbivore treatment. Error bars represent \pm SE.

672 **Fig. 7.** A conceptual model showing the reciprocal interactions between caterpillars and yak
673 or Tibetan sheep by changing food resources or habitat structure based on their diet preferences.
674 The + and - symbols indicate positive and negative effects, respectively. The upwards arrows
675 and downwards arrows indicate increase and decrease, respectively. Dashed lines mean
676 mechanisms, and solid lines mean results (positive or negative effects). Blue lines indicate the
677 effects of large herbivores on caterpillars and green lines mean that caterpillars on large
678 herbivores.

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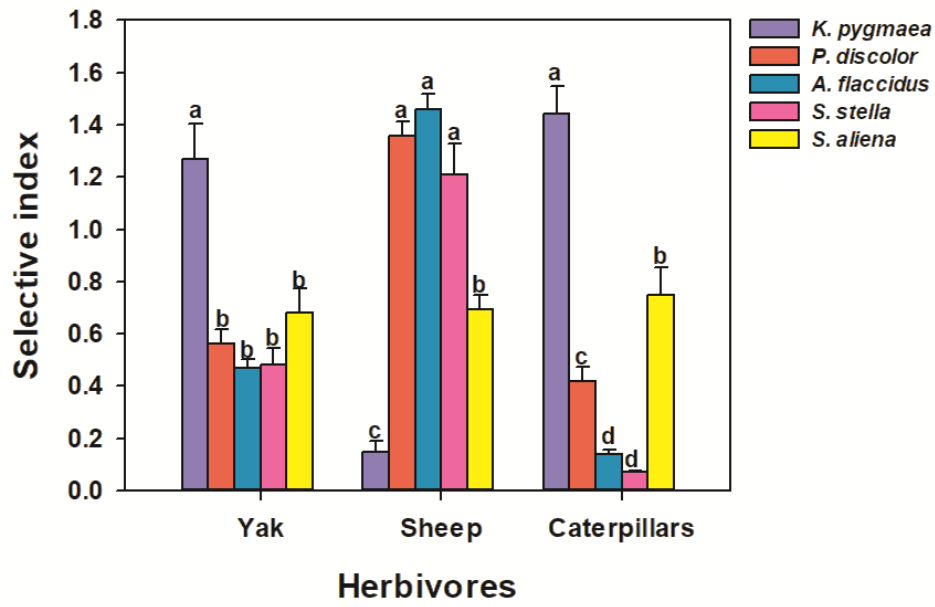
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698 **Fig. 1**



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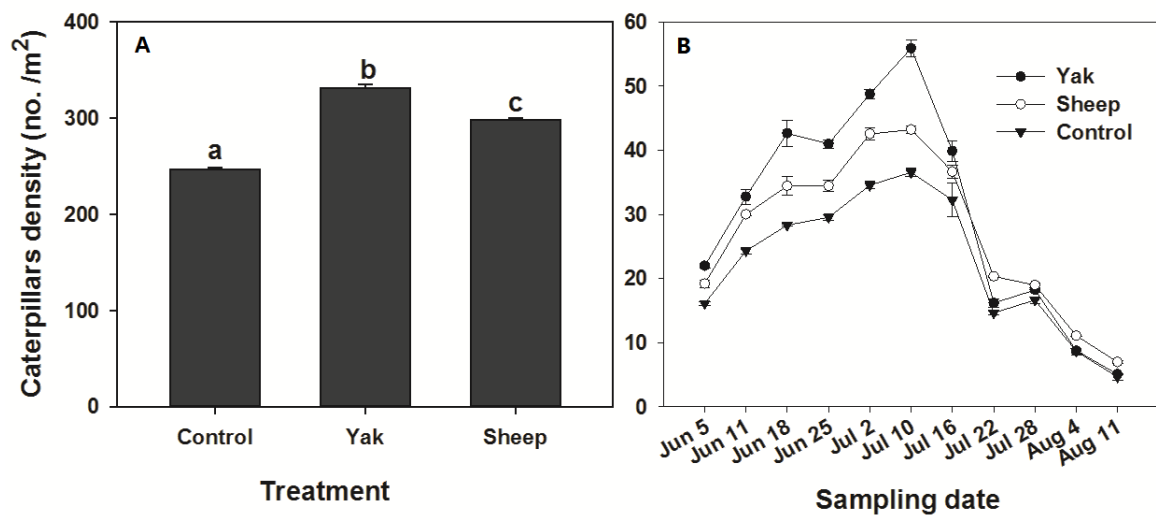
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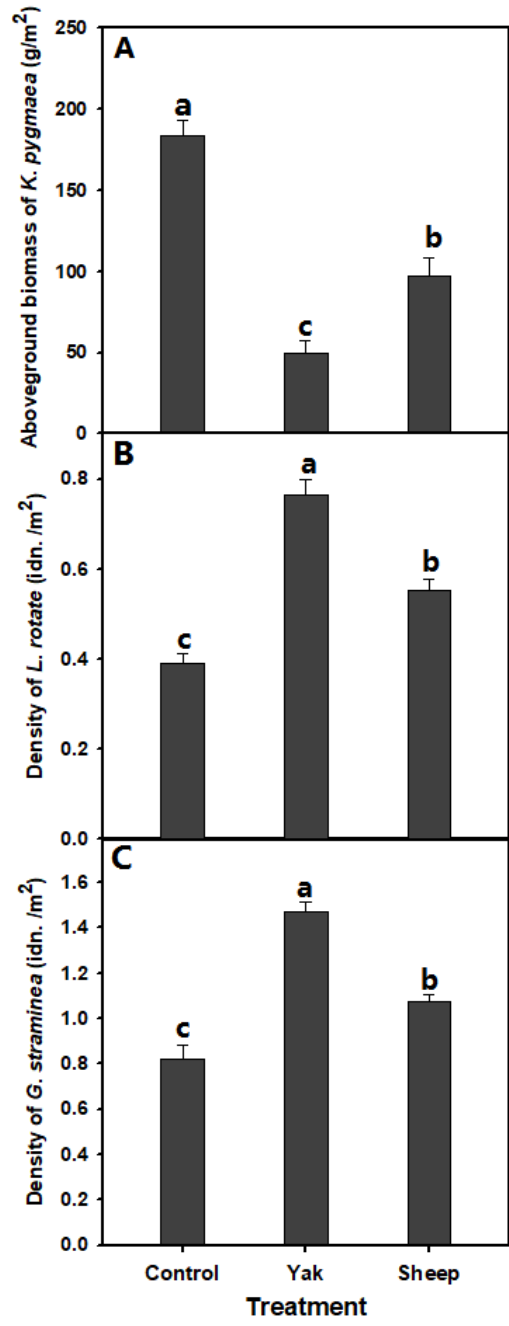
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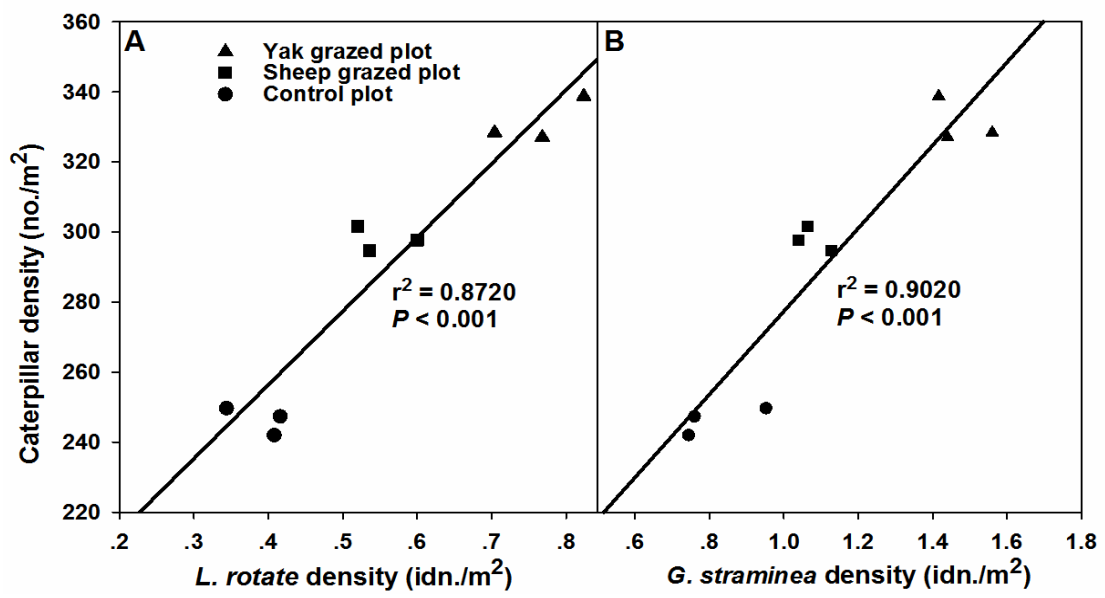
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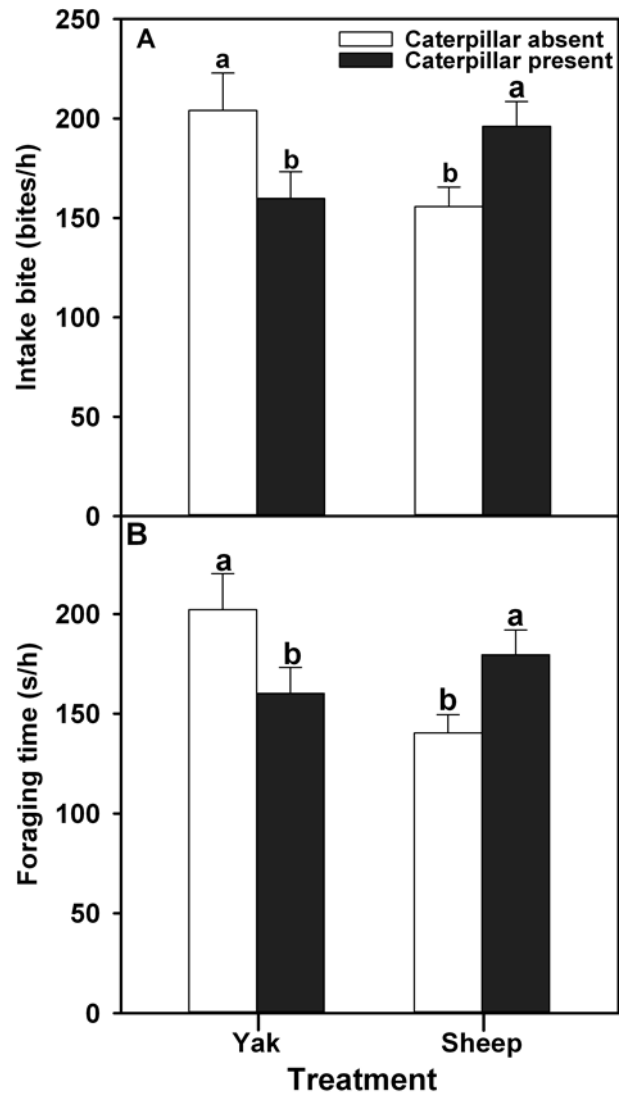
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750 Fig. 5



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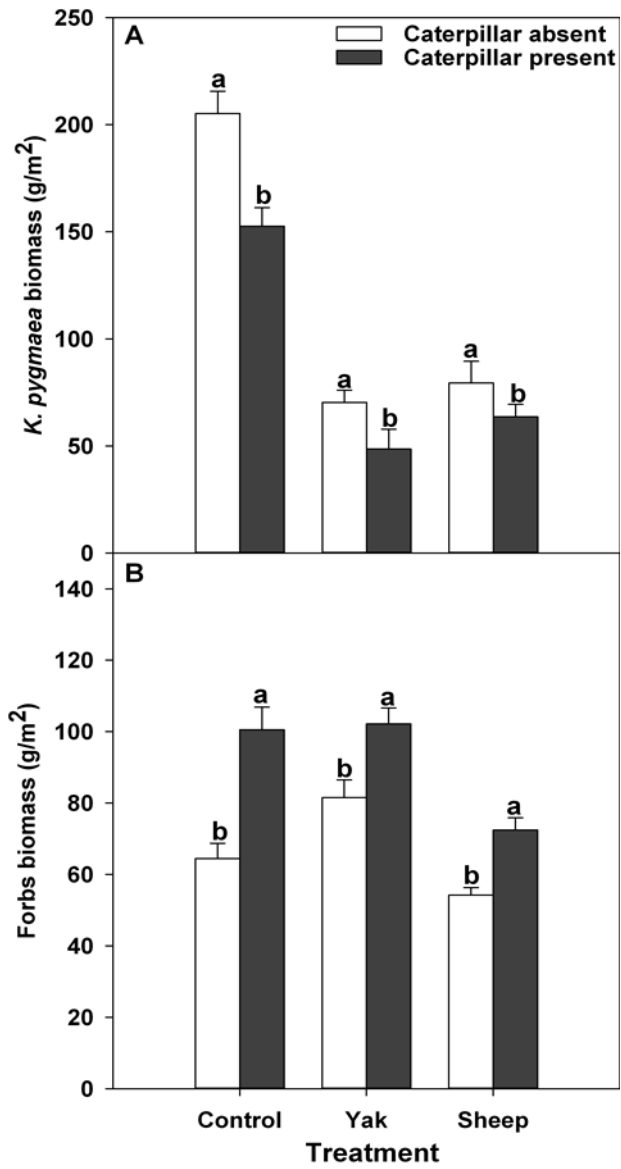
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760 **Fig. 6**



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769 **Fig. 7**

