Food and habitat provisions jointly determine competitive and facilitative interactions among distantly related herbivores.

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Abstract

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

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

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

4. Synthesis. Our study indicates that two different mechanisms (the changes in habitat and food availability) induced by herbivore jointly determine competitive and facilitative interactions between distantly related herbivore species. We also suggest that examining the
bidirectional effects between herbivores offers a better understanding of competition and facilitation in terrestrial animal communities.

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

INTRODUCTION

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

In recent decades, interspecific interactions among distantly related herbivores have been increasingly identified, and both competition (Denno et al. 1995; Ohgushi 2005; Wilkerson et al. 2013) and facilitation (Kuijper et al. 2008; Bakker et al. 2009) have been found. However, the majority of such studies have classically investigated the effects of large herbivores on smaller ones (Enans et al. 2006; Pringle 2007; Poelman et al. 2008). For example, large
mammalian herbivores depress small rodents or invertebrate herbivores that rely on host plants in the Africa savanna (Keesing 1998), an alpine meadow (Steen et al. 2005), and a coastal dune community (Huntzinger & Lawton 2008). Additionally, larger herbivores successively facilitate smaller herbivores by improving or stimulating growth of higher quality forage (Gordon 1988). Since the concept of ‘indirect interaction webs’ was presented (Ohgushi 2005), ecologists found that small herbivores such as herbivorous insects are an overlooked, but potentially important factor that indirectly influenced the foraging behavior of large herbivores. For example, a species of caterpillar increased a pika’s actively selected areas (Barrio et al. 2013), and grasshoppers benefitted sheep’s foraging time during the peak of vegetation growing season (Zhong et al. 2014). Despite these suggestive results, the mechanisms to answer how small herbivores alter large herbivore performance, especially how insect herbivores affect mammalian herbivores, remains fragmentary at best.

Herbivores may interact with each other via a variety of mechanisms, and they may engage in some combination of competition or facilitation when they both share the same plant resources or occupy the same space. Experimental investigations across different habitats have revealed that herbivores affect each other mainly by two key aspects: trophic resource availability (McNaughton 1976; Murray & Illius 2000) and habitat structure (Torre et al. 2008; Woodcock & Pywell 2009; Sendoya & Oliveira 2015). One herbivore species can induce plant compensatory growth by foraging and cause changes in the quantity or quality of its host plant, thus having important consequences for another herbivore species using the same host (McNaughton 1983; Odadi et al. 2011). Some herbivore species can act as ‘ecosystem engineers’ through their foraging, trampling, burrowing activities (Jones et al. 1997), and
strongly modify the habitat structure for other species (Davidson et al. 2007; Bakker et al. 2009). Some larger herbivorous insects like leaf-rolling caterpillars benefit small aphids by providing utilizing leaf shelters (Nakamura & Ohgushi 2003). Additionally, herbivores can interact with each other through sharing the same natural enemies, which could increase or decrease the predation risk (Holt & Lawton 1994; Schmitz 2008). Moreover, herbivores may affect each other by direct means (Gish et al. 2017; Berman et al. 2017). For example, in the semi-natural grasslands of the Netherlands, high grazing intensity of sheep increased the nest damage and mortality of the caterpillars by incidental ingestion (van Noordwijk et al. 2012).

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

Here, we conduct a set of manipulative field experiments to examine the simultaneous effects among two large vertebrate herbivores (yak and Tibetan sheep) and an insect herbivore (caterpillars) with different diet preferences to evaluate the competitive or facilitative interactions among them. Previous works have shown that caterpillars and yak prefer to consume the dominant sedge Kobresia pygmaea (Wan & Zhang 2006; Ding et al. 2006), we
therefore hypothesized that caterpillars and yak exert a competitive interaction because of food competition between them. In contrast, Tibetan sheep prefer forbs (Ding et al. 2006). Caterpillars’ preference for dominant sedge *K. pygmaea* might reduce the competition to forbs, thus increase biomass of forbs and thereby facilitate Tibetan sheep’s foraging for preferred forbs. Similarly, sheep’s preference for forbs might further facilitate Caterpillars’ foraging for *K. pygmaea* due to release of competition. We therefore hypothesized that caterpillars and Tibetan sheep exert a facilitative interaction. Additionally, the caterpillars prefer to live in two broad-leaf forbs, *Lamiophlomis rotata* and *Gentiana straminea* (D. Pan & X. Li, personal observations, Supplementary, Fig. S1), which were never eaten by yak or Tibetan sheep (Supplementary, Table. S1). Therefore, grazing by yak and Tibetan sheep might release the completion of the two broad-leaf forbs, which could increase their densities and potentially improve habitat for caterpillars. We tested these hypotheses by measuring consumer and vegetation responses to various combinations of herbivores, and then discuss the underlying mechanisms related to habitat and food resources availability based on herbivore diets.

**MATERIALS AND METHODS**

*Study site and background*

We conducted our research at the Alpine Grassland Ecological Research Station of Tsinghua University-Qinghai University located in Qinghai-Tibetan plateau (33°20’ N, 97°25’ E, 4290 m above sea level), Qinghai Province, China for 2 years. This study site has a continental alpine climate, with severe and long winters and short cool summers. The annual mean
temperature is around -4.4°C (ranging from -13.3°C in January to 9.2°C in July), and annual mean precipitation is about 430 mm, with 70% falling in June-August. The soil is classified as Mat Cry-gelic Cambisols (Cao et al. 2004).

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

**Experimental design and management**

We established a manipulative field grazing experiment in the study site in 2013. The experiment employed a randomized block design and consisted of nine plots with similar vegetation characteristics and initial caterpillars densities arranged in three blocks of three (measured before the experiment, see Table S2). The blocks were parallel to each other, with a distance of 50 m from neighboring blocks. Each plot was 100 × 100 m in size and fenced with barbed wire. Neighboring plots within blocks were separated by 30 m (see Fig. S2). Each
A plot within a block was randomly assigned to receive one of the following treatments: yak grazed, Tibetan sheep grazed, and vertebrates excluded (control). Grazing was maintained at a moderate intensity in each herbivore treatment (approximate 50% of aboveground plant biomass removal during the growing season; stocking rate was about 6.17 sheep ha\(^{-1}\)). The manipulated grazing season was similar to the season for free grazing in this region: from the second week of June through the last week of September. Grazing activity lasted for 12 hours (from 06:00 h to 18:00 h) on each day.

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

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

In August 2014, we measured the diet selection of large herbivores at the plot scale. Four 40-m linear transects were laid out in each grazed plot (except in the four pairs of 5 × 5 m subplots),
and ten 0.5 × 0.5 m quadrats spaced 4 meters apart were placed along each transect. We measured the percentage of plant species (P) of each transect. We recorded and assigned with a value of one for each plant species in the quarter, and then summed the values of each species per transect (each recorded species of the transect obtained a value from 1 to 10, marked with ‘V’). The percentage of each species among all recorded species in the transect was calculated by the following equation: \( P = \frac{V_i}{\sum_{i=1}^{n} V_i} \), where \( V_i \) is the summed value of the species \( i \) in the transect, and \( n \) is the number of all recorded species in the transect. Additionally, we measured the grazing frequency (GF) of each plant species fed by the herd in the transect. We recorded species fed by the animals by indirect observations (direct observations were not possible because yak and Tibetan sheep did not allow close approach). We waited until the herd had fed and moved away from the quarter, and then visited the quarter and recorded the eaten species from the feeding signs (Mishra et al. 2004). This allowed identification of plant species fed upon by the animals (Supplementary: Fig. S3). We assigned with a value of one for grazed plant species, and zero for untouched species in the quarter. We summed the values of each plant species per transect (each plant species in the transect obtained a value from 0 to 10, marked with ‘GV’). The grazing frequency of each plant species in the transect was calculated by the following equation: \( GF = \frac{GV_i}{\sum_{i=1}^{n} GV_i} \), where \( GV_i \) is the summed value of the species \( i \) in the transect, and \( n \) is the number of species recorded in the transect. We used selectivity index (SI) to describe diet preference of yak and Tibetan sheep. SI was calculated based on the following equation: \( SI = \frac{GF}{P} \). The average SI for the four transects in each plot was then used in analyses.

On a sunny day in early August 2014, we investigated the diet selection of caterpillars.
Firstly, the percentage of plant species (P) in each ungrazed plot were measured by using the same method with grazed plot (see above). We then investigated the percentage of feeding time (PFT) of the species fed by caterpillars. We randomly chose nine caterpillars from ungrazed plots (three caterpillars in each plot) and installed an identifying red paint mark on their backsides and abdomens to facilitate observation. We recorded the caterpillars’ feeding time on different plant species, and all individuals were observed for eight hours continuously from 09:00 to 17:00. The percentage of feeding time (PFT) of the species fed by caterpillars was calculated using the following equation: 
\[ PFT = \frac{\sum_{i=1}^{n} FT_i}{P} \]
where \( FT_i \) is the total feeding time of the plant species \( i \) for the observation period, and \( n \) is the number of species fed by caterpillars. The selectivity index (SI) was calculated based on the following equation:
\[ SI = \frac{PFT}{P} \]
We used the average SI for the three caterpillars in each plot for the analyses.

**Effects of large herbivores on caterpillars’ density**

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

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

In mid-August 2014, we measured the biomass of the dominant species *K. pygmaea* in twelve
0.5 × 0.5 m quadrats along the two diagonal lines in each plot. We clipped, dried, and weighted the plants at 60°C for 48 h to estimate plant biomass per square meter.

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

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

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

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

**Statistical analyses**

All analyses were performed with software R version 3.5.3 (R Core Team 2019). We used linear mixed effect models (LMMs) from the lme4 package (Bates *et al* 2015) to test the effects
of grazing on caterpillars and plants. Biomass of *K. pygmaea*, density of *L. rotata* and *G. straminea* were included as response variables separately. Grazing treatment (three levels: control, sheep and yak) was included as a fixed factor, block and nested sampling replicates as random factors. Tukey tests between treatments comparisons were performed by multcomp package (Hothorn et al. 2008) after each LMM. For dynamics of caterpillars (density in weekly sampling time), we performed a repeated measures LMM (with grazing treatment, sampling time and their interaction as fixed factors; plot ID of each treatment within block (e.g. ‘block1-yak’) and sampling time as random effects, where time was also treated as a temporal autocorrelation structure of order one-corAR1 in the model). To test the relationship between caterpillars and the broad-leaf forbs, we used a simple linear model to regress the total caterpillars’ density against the density of plant species including *L. rotata* and *G. straminea* separately by all plot-scale samplings in the site. To test the impacts of caterpillars on plants (including biomass of *K. pygmaea* and forbs comprising *A. flaccidus*, *P. sibiricum*, and *S. stella*) within each grazing treatment plots separately, we used LMMs with caterpillars treatment (two levels: removed and control) as a fixed effect while block and paired subplots as random effects. To test the impacts of caterpillars on large-herbivore foraging behaviors (including intake bites and foraging time), we used LMMs with caterpillars treatment as a fixed effect while block, paired subplots and also large herbivore individual (considering the possible foraging variation between individuals) as random effects. For all models, residual plots were visually inspected to ensure no obvious deviations from homoscedasticity or normality. If not, response variables were transformed by log or square root to meet the model assumptions.
RESULTS

Diet selection of large herbivores and caterpillars

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

Effects of large herbivores on caterpillars’ density

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

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

Yak and Tibetan sheep had significant effects on aboveground biomass of food resources, *K. pygmaea*, for the caterpillars (Fig. 3A). The biomass of *K. pygmaea* was consistently lower on grazed plots than ungrazed plots in August 2014 (*F* = 115.99, df = 2, 60, *P* < 0.001; Fig. 3A).
The biomass of *K. pygmaea* on yak and sheep grazed plots were only 27% and 53% compared with the control. Additionally, yak grazed plots had significant lower biomass of *K. pygmaea* than sheep grazed plots.

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

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

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

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

Caterpillars had opposite effects on the foraging behavior of yak and sheep (Fig. 5). The foraging time and intake bites of yak significantly decreased in the subplots in the presence of caterpillars (foraging time: *F* = 6.70, df = 1, 23, *P* = 0.016; Fig. 5A; intake bites: *F* = 6.92, df = 1, 23, *P* = 0.015; Fig. 5B). The foraging time and intake bites of yak were 18% and 20% lower in caterpillar-present subplots respectively than caterpillar-absent subplots. In contrast,
Tibetan sheep had significant higher foraging time and intake bites in the subplots where caterpillars remained (foraging time: $F = 18.75, \text{df} = 1, 23, P < 0.001$; Fig. 5A; intake bites: $F = 14.97, \text{df} = 1, 23, P < 0.001$; Fig. 5B). The foraging time and intake bites of sheep were 22% and 20% higher in caterpillars’ present subplots respectively than caterpillar-’ absent subplots.

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

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

**DISCUSSION**

Our results suggest that the caterpillars exerted a positive interaction with Tibetan sheep and a negative interaction with yak, and demonstrate the bi-directional effects between distantly related herbivore species in our system. Most previous studies on potential interactions between distantly related herbivores have examined the effects of vertebrate herbivores on insect herbivores, and announced a facilitation or competition based on the outcome (see
Introduction. In this study, both yak and Tibetan sheep had a positive effect on the density of caterpillars (Fig. 2), which traditionally would be identified as a facilitation interaction between the vertebrate and invertebrate herbivores if only the effect in one direction was considered. However, we found that caterpillars posed a significant positive effect on Tibetan sheep while a negative effect on yak due to diet differences between yak and sheep (Fig. 5). Caterpillars and sheep demonstrated a two-way facilitation, while caterpillars and yak demonstrated facilitation for the insect and competition towards the mammal. Our study therefore provides evidences of the complexity of interactions between distantly related herbivores by testing bi-directional effects in terrestrial animal communities.

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

**Effects of vertebrate herbivores on insect herbivores**

The positive effects of large herbivores-yak and sheep on insect herbivore-caterpillars in this study, was a result of the increased food availability or habitat modification. However, we found that yak grazing significantly reduced the biomass of *K. pygmaea* as predicted due to its high preference for *K. pygmaea* (Fig. 1). Furthermore, Tibetan sheep grazing also reduced the biomass of *K. pygmaea* (Fig. 3A). The large herbivore foraging-induced reduction in biomass of *K. pygmaea*, the most important food source for caterpillars, therefore could
negatively affect density of caterpillars due to reduced food availability. Thus, the altered food
resources for the caterpillars cannot explain the indirect positive effects of large herbivores on
caterpillars. In our study system, *L. rotata* and *G. straminea* are the main shelter habitat for
caterpillars. As predicted, both yak and Tibetan sheep grazing significantly increased the
densities of the two broadleaf forbs, which could positively affect density of caterpillars (Fig.
3B, C). We also found that the densities of the two plant species were significantly and
positively related to that of the caterpillars (Fig. 4). Therefore, relative to available food
resources, habitat could be more important in mediating the net effects of large vertebrate
herbivores on insect herbivores. Previous studies also found that large herbivores pose great
impacts on habitat structure of smaller species through feeding or trampling activities (Frago
*et al.* 2012; Berman *et al.* 2018).

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

*Effects of insects herbivores on vertebrate herbivores*

The effects of insects herbivores on larger herbivores have received less attention, and usually reported when the herbivorous insects constitute a pest (Musser *et al.* 2002; Berman *et al.* 2017). An early study showed that caterpillars increased pika’s foraging activity in Canada alpine tundra (Barrio *et al.* 2013), and grasshoppers benefited sheep’s access to palatable forbs in the eastern region of the Eurasian Steppe Zone (Zhong *et al.* 2014), but the underlying mechanisms remained unexplored or limited. With the exception of insect outbreaks, herbivorous insects are deemed to typically consume a small fraction of the available plant foliage and thus have little impact on plant population dynamics (Crawley 1989). Also, the biomass removal by herbivorous insects is likely to be non-significant relative to large herbivores (Demment & van Soest 1985; Illius & Gordon 1992). However, there is a growing evidence indicating that small herbivores such as insects can alter competition abilities of plants and primary productivity at a local scale (Rees & Brown 1992; Schädler *et al.* 2007; Kim *et al.* 2013; Loïc *et al.* 2018), and they rapidly influence the vegetation characteristics when their densities are relative high (Zhang *et al.* 2011). In our study site, the total density of caterpillars during the experiment period was very high (exceeded 250 no. /m², Fig. 2A). As expected, the caterpillars reduced the biomass of the dominant species, *K. pygmaea* (Fig. 6A), the main food resource for yak and caterpillars, thus negatively affecting yak foraging. Nevertheless, caterpillars’ preference for *K. pygmaea* increased the biomass of forb species *A. flaccidus*, *P. sibiricum* and *S. stella*, as the main food for Tibetan sheep, thereby increasing the
available food resources for sheep. Therefore, in this study the caterpillars indirectly facilitated sheep grazing and competed with yak by distinctively changing available food quantity for large herbivores-yak and sheep. However, we are not sure whether insect herbivory could change the chemical composition of food plants, such as altering nutritive value, and thus affecting other herbivores.

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

**CONCLUSIONS**

Testing the bi-directional effects between herbivores is necessary to understand the structure of herbivore assemblages and the facilitative or competitive interactions between them. Distantly related herbivores affect each other in different ways: large herbivores affect small herbivore insects mainly through modifying habitat structure and small herbivore insects affect larger herbivores by changing their food quantity (Fig. 7). Our study indicates that interactions between distantly related herbivorous species in terrestrial animal communities are complex and that animal diet preference is viewed as a good predictor for the facilitative or competitive
interaction between distantly related herbivores. Clearly, examining the effects of herbivores on each other simultaneously is essential to our understanding of competition and facilitation in terrestrial animal communities.

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AUTHOR CONTRIBUTIONS

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

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**Figure legends**

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

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

**Fig. 3.** Effects of large herbivores on the main food resources and habitat of caterpillars.
Biomass of *K. pygmaea* (A), density of *L. rotata* (B), and density *G. straminea* (C). Different letters above the bars indicate significant difference at $P < 0.05$. Error bars represent ± SE.

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

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

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

**Fig. 7.** A conceptual model showing the reciprocal interactions between caterpillars and yak or Tibetan sheep by changing food resources or habitat structure based on their diet preferences. The + and - symbols indicate positive and negative effects, respectively. The upwards arrows and downwards arrows indicate increase and decrease, respectively. Dashed lines mean mechanisms, and solid lines mean results (positive or negative effects). Blue lines indicate the effects of large herbivores on caterpillars and green lines mean that caterpillars on large herbivores.
Fig. 2
Fig. 3
Fig. 5

- **A**: **Yak grazed plot**
- **B**: **Sheep grazed plot**
- **C**: **Control plot**

- **L. rotate density (idn./m²)**
- **G. straminea density (idn./m²)**

- $r^2 = 0.8720\quad P < 0.001$
- $r^2 = 0.9020\quad P < 0.001$
Fig. 6
Fig. 7