Received: 12 April 2019 | Accepted: 9 September 2019
DOI: 10.1111/1365-2435.13456

RESEARCH ARTICLE

Functional Ecology BRITISH ECOLOGICAL SOCIETY

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

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Funding information
National Natural Science Foundation of China, Grant/Award Number: 31772652 and 31770520; Program for Introducing Talents to Universities, Grant/Award Number: B16011; National Key Research and Development Program of China, Grant/Award Number: 2016YFC0500602; Ministry of Education Innovation Team Development Plan, Grant/Award Number: 2013-373

Handling Editor: Clare McArthur

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: an insect caterpillar (*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 but increased Tibetan sheep 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-feeding upon *Lamiophlomis rotata* and *Gentiana straminea*, the caterpillars preferred habitat, increased densities of the two plant species, thus favouring the caterpillars. In turn, the caterpillar preference for *Kobresia pygmaea* significantly reduced food resources for yak, while promoting food resources (multiple forbs) for sheep.
4. *Synthesis*. Our study indicates that two different mechanisms (the changes in habitat and food availability) induced by herbivore foraging jointly determine competitive and facilitative interactions between distantly related herbivore species. We also suggest that examining the bi-directional 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*

1 | INTRODUCTION

Interactions among herbivores play a central role in maintaining community structure and ecological functioning (Kimuyu et al., 2017; Koerner et al., 2018; Strauss, 1991). However, the vast majority of studies of herbivore–herbivore interactions only consider affects in one direction (Odadi, Karachi, Abdulrazak, & Young, 2011; Bakker, Doerescu, Straile, & Holmgren, 2013, but see Zhong et al., 2014; Dangles, Herrera, Carpio, & Lortie, 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 have a 'bi-directional effect', and facilitation is identified only when encounters between organisms benefit at least one of the participants and cause harm to neither (Bruno, Stachowicz, & Bertness, 2003). Therefore, simultaneously examining the effects of herbivores on each other can give us a clearer understanding of competition versus facilitation in ecological animal communities.

In recent decades, interspecific interactions among distantly related herbivores have been increasingly identified, and both competition (Denno, McClure, & Ott, 1995; Ohgushi, 2005; Wilkerson, Roche, & Young, 2013) and facilitation (Bakker, Olff, & Gleichman, 2009; Kuijper, Beek, Wieren, & Bakker, 2008) have been found. However, the majority of such studies have classically investigated the effects of large herbivores on smaller ones (Poelman, Broekgaarden, Loon, & Dicke, 2008; Pringle, 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, Mysterud, & Austrheim, 2005) and a coastal dune community (Huntzinger & Cushman, 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 behaviour of large herbivores. For example, a species of caterpillar increased a pika's actively selected areas (Barrio, Hik, Peck, & Bueno, 2013), and grasshoppers benefitted sheep 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 ways: trophic resource availability (McNaughton, 1976; Murray & Illius, 2000) and habitat structure (Sendoya & Oliveira, 2015; Torre et al., 2007; Woodcock & Pywell, 2009; Davidson et al., 2010). 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 and burrowing activities (Jones, Lawton, & Shachak, 1997) and strongly modify the habitat structure for other species (Bakker et al., 2009; Davidson & Lightfoot, 2007; Li et al., 2019). Some larger herbivorous insects like leafroller caterpillars benefit small aphid by providing 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 (Berman, Ben-Ari, Glasser, Gish, & Inbar, 2017; Gish, Ben-Ari, & Inbar, 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, Flierman, Remke, Wallisdevries, & Berg, 2012).

The Qinghai-Tibetan plateau, known as 'the third pole' in the world, extends 2.5 million km^2, 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 alpherakii*, 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* (Ding, Long, Wang, & Shang, 2006; Wan & Zhang, 2006). We 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). Caterpillar preference for dominant sedge *K. pygmaea* might reduce the plant–plant competition with forbs, thus increase biomass of forbs and thereby facilitate Tibetan sheep foraging for preferred forbs. Similarly, sheep preference for forbs might further facilitate caterpillars foraging for *K. pygmaea*, which may be released from forb competition. We therefore hypothesized that caterpillars and Tibetan sheep exert a facilitative interaction. Additionally, the caterpillars prefer to live in two broadleaf forbs, *Lamiophlomis rotata* and *Gentiana straminea* (personal observations, see Figure S1), which were rarely eaten by yak or Tibetan sheep (Table S1). Therefore, grazing by yak and Tibetan sheep for other plant species might release the competition with the two broadleaf forbs, which could increase their density 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 resource availability based on herbivore diets.

2 | MATERIALS AND METHODS

2.1 | 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, 4,290 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 broadleaf 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 (Figure 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, Wang, & Liu, 2006).

2.2 | 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 caterpillar 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 neighbouring blocks. Each plot was 100 × 100 m in size and fenced with barbed wire. Neighbouring plots within blocks were separated by 30 m (see Figure S2). Each 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 above-ground plant biomass removal during the growing season), which was achieved by 9 yaks (c. 350 kg) in yak-grazed plot and 45 Tibetan sheep (c. 50 kg) in sheep-grazed plot. 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 hr (from 06:00 hr to 18:00 hr) 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 Figure 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 of water) which was effective 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 caterpillar exclusion manipulation was from the third week of May through the second week of August. The manipulation was repeated in 2014.

2.3 | Diet preference 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 metres 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, denoted ‘V’). The percentage of each species among all recorded species in the transect was calculated by the following equation: $P = V_i/\Sigma_{i=1}^{n}Vi$, 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 eaten by the herd in the transect. We recorded species eaten 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, Wieren, Ketner, Heitkönig, & Prins, 2004, see Figure S3). This allowed an identification of plant species fed upon by the animals. 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, denoted ‘GV’). The grazing frequency of each plant species in the transect was calculated by the following equation: $\mathrm{GF} = \mathrm{GV}_i/\Sigma_{i=1}^{n}\mathrm{GV}_i$, 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 a selectivity index (SI) to describe diet preference of yak and Tibetan sheep. SI was calculated based on the following equation: SI = 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) on each species eaten by caterpillars. We randomly chose nine caterpillars from ungrazed plots (three caterpillars in each plot) and installed an identifying red paint mark on their backs and abdomens to facilitate observation. We recorded the caterpillar feeding time on different plant species, and all individuals were observed for 8 hr continuously from 09:00 to 17:00. The percentage of feeding time (PFT) on each species eaten by caterpillars was calculated using the following equation: $\mathrm{PFT} = \mathrm{FT}_i/\Sigma_{i=1}^{n}\mathrm{FT}_i$, where FT_i is the total feeding time on plant species i for the observation period, and n is the number of species eaten by caterpillars. The selectivity index (SI) was calculated based on the following equation: SI = PFT/P. Similarly, the SI represented preference of caterpillars. We used the average SI for the three caterpillars in each plot for the analyses.

2.4 | Effects of large herbivores on caterpillar density

From 5 June to 11 August 2014, we surveyed caterpillar 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 × 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.

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

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

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 of the two species per square metre.

2.6 | Effects of caterpillars on the foraging behaviour and food resources of large herbivores

In early August 2014, we measured the foraging time (total seconds within the hour that the herbivores fed) and intake bites (bites within the hour that the herbivores fed) by yak and Tibetan sheep in each subplot in the large herbivore-grazed plots. The observations of large herbivore foraging behaviours were conducted twice daily (08:00–10:00 in the morning and 15:00–17:00 in the afternoon), for a total of 4 hr each day. The observations lasted for 3 days. The total foraging time and intake bites for a continuous 2 hr 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.

2.7 | Statistical analyses

To test the diet preference (selectivity index) of large herbivores and caterpillars, we used linear mixed effect model (LMM) with selectivity index included as response variables and plant species as a fixed effect while block as a random effect for each herbivore separately; multiple comparisons between plant species were performed by Tukey tests for each herbivore. We used LMMs to test the effects of large herbivore grazing on caterpillars and plants; total density of caterpillars and biomass of *K. pygmaea*, density of *L. rotata* and *G. straminea* were included as response variables separately; grazing treatment was included as a fixed factor and block as a random factor; Tukey tests between treatments comparisons were performed after each LMM. To test the relationship between caterpillars and the broadleaf forbs, we used a simple linear model to regress the total density of caterpillars against the density of plant species including *L. rotata* and *G. straminea* separately with all plot-scale samplings in the site. To test the impacts of caterpillars on plants (including biomass of *K. pygmaea* and the three forbs comprising *A. flaccidus*, *Polygonum sibiricum* and *S. stella*) within each grazing treatment plots (control, yak grazed and sheep grazed) separately, we used LMMs with caterpillar treatment as a fixed effect while block and paired subplots as random effects. To test the impacts of caterpillars on large herbivore foraging behaviours (including intake bites and foraging time), we used LMMs with caterpillar treatment as a fixed effect while block and large herbivore individual (considering the possible foraging variation between individuals) as random effects for each herbivore species separately. 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. All analyses were performed with software R version 3.5.3 (R Core Team, 2019).

3 | RESULTS

3.1 | Diet preference of large herbivores and caterpillars

Diet preference of yak and Tibetan sheep differed substantially in our study site (Figure 1). 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: 0.68 ± 0.11, 0.56 ± 0.04, 0.48 ± 0.04 and 0.47 ± 0.04, respectively). In contrast, Tibetan sheep preferred the forbs, *A. flaccidus*, *P. discolor* and *S. stella* (SI: 1.46 ± 0.06, 1.36 ± 0.06

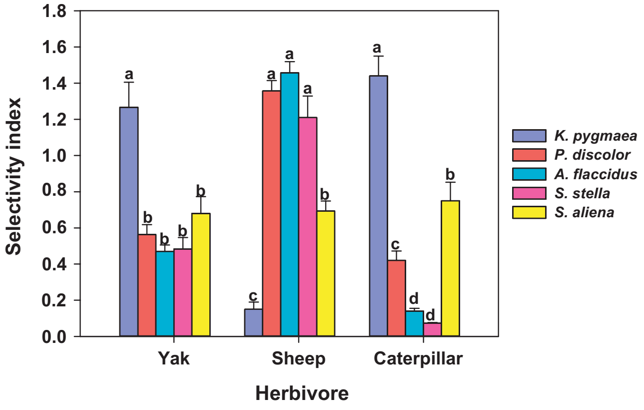

FIGURE 1 Selectivity index of the main plant species foraged by yak, sheep and caterpillars. Different letters above the bars indicate significant difference for each herbivore at $p < .05$. Error bars represent ± *SE*. Value of selectivity index above 1 means preferred select, equal 1 means neither preferred nor against, and below 1 means selected against

and 1.21 ± 0.11, respectively). Caterpillars predominantly consumed *K. pygmaea* (SI: 1.44 ± 0.11; Figure 1).

3.2 | Effects of large herbivores on caterpillar density

The density of caterpillars was significantly affected by the large herbivores ($F = 226.40$, $df = 2, 4$, $p < .001$). Large herbivore plots had significantly higher caterpillar densities compared with ungrazed plots (Figure 2a). The total density of caterpillars was 35% and 21% higher in yak- and Tibetan sheep-grazed plots, respectively, than the control. The dynamics of caterpillar density showed a clear pattern over time and generally increased from 5 June to 10 July to a peak level and then sharply declined by 11 August (Figure 2b).

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

Yak and Tibetan sheep had significant effects on above-ground biomass of food resources, *K. pygmaea*, for the caterpillars (Figure 3a). The biomass of *K. pygmaea* was consistently lower on grazed plots than ungrazed plots in August 2014 ($F = 52.92$, $df = 2, 4$, $p = .001$; Figure 3a). The biomass of *K. pygmaea* on yak- and sheep-grazed plots was 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 ($F = 46.02$, $df = 2, 4$, $p = .002$, for *L. rotata*; $F = 45.49$, $df = 2, 4$, $p = .002$, for *G. straminea*; Figure 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.

3.4 | 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* (adjusted $R^2 = 0.888$, $F = 64.44$, $df = 1, 5$, $p < .001$; Figure 4a) and *G. straminea* (adjusted $R^2 = 0.854$, $F = 47.68$, $df = 1, 5$, $p = .001$; Figure 4b) in the nine plots.

3.5 | Effects of caterpillars on the foraging behaviour of larger herbivores

Caterpillars had opposite effects on the foraging behaviour of yak and sheep (Figure 5). The foraging time and intake bites of yak significantly decreased in the subplots in the presence of caterpillars (foraging time: $F = 6.70$, $df = 1, 23$, $p = .016$; Figure 5a; intake bites: $F = 6.91$, $df = 1, 23$, $p = .015$; Figure 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: $F = 18.75$, $df = 1, 23$, $p < .001$; Figure 5a; intake bites: $F = 14.97$, $df = 1, 23$, $p < .001$; Figure 5b). The foraging time and intake bites of sheep were 22% and 20% higher in caterpillar-present subplots, respectively, than caterpillar-absent subplots.

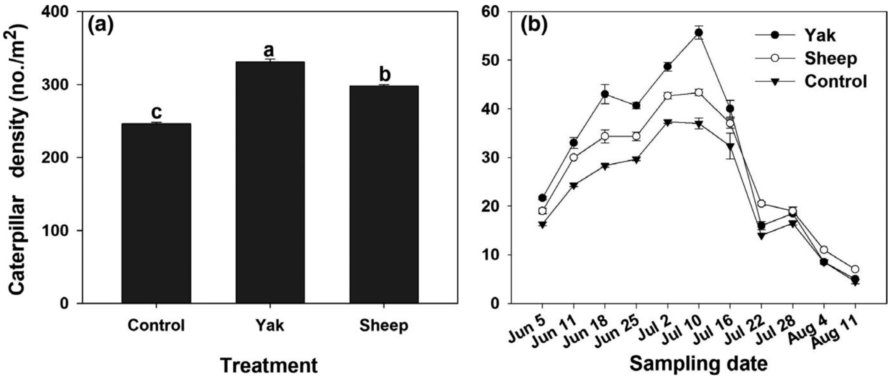

FIGURE 2 Density of caterpillars. (a) Total density in different herbivore-grazed plots. (b) The dynamic of caterpillar density in different herbivore-grazed plots during the study period. Different letters above the bars indicate significant difference at $p < .05$. Error bars represent ± *SE*

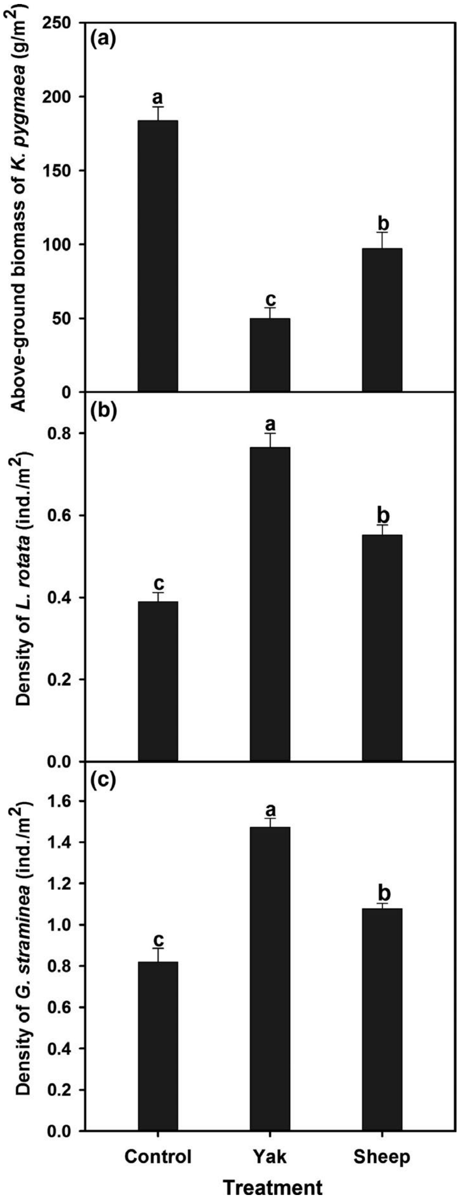

FIGURE 3 Effects of large herbivores on the main food resources and habitat of caterpillars. Biomass of *Kobresia pygmaea* (a), density of *Lamiophlomis rotata* (b) and density *Gentiana straminea* (c). Different letters above the bars indicate significant difference at $p < .05$. Error bars represent ± *SE*

3.6 | Effects of caterpillars on available food resources of large herbivores

Caterpillars had significant but opposite effects on the biomass of *K. pygmaea* and forbs (Figure 6). The biomass of *K. pygmaea* was significantly lower when caterpillars were present in the subplots of the all plots ($F = 25.12$, $df = 1, 11$, $p < .001$; Figure 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 ($F = 200.69$, $df = 1, 11$, $p < .001$; Figure 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.

4 | 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 above). In this study, both yak and Tibetan sheep had a positive effect on the density of caterpillars (Figure 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 (Figure 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 evidence 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 by 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 affected the insect herbivore by modifying habitat, while insect herbivore affected large herbivores by changing the available food quantity.

4.1 | Effects of vertebrate herbivores on insect herbivores

The positive effects of large herbivores (yak and sheep) on insect herbivores (caterpillars) in this study were initially hypothesized 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* (Figure 1). Furthermore, Tibetan sheep grazing also reduced the biomass of *K. pygmaea* even though it was seldom selected (Figure 3a). The large herbivore foraging-induced reduction in biomass of *K. pygmaea*, the most important food source for caterpillars, therefore could have negatively affected density of caterpillars yet it did not. Thus, altered (i.e. reduced) 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

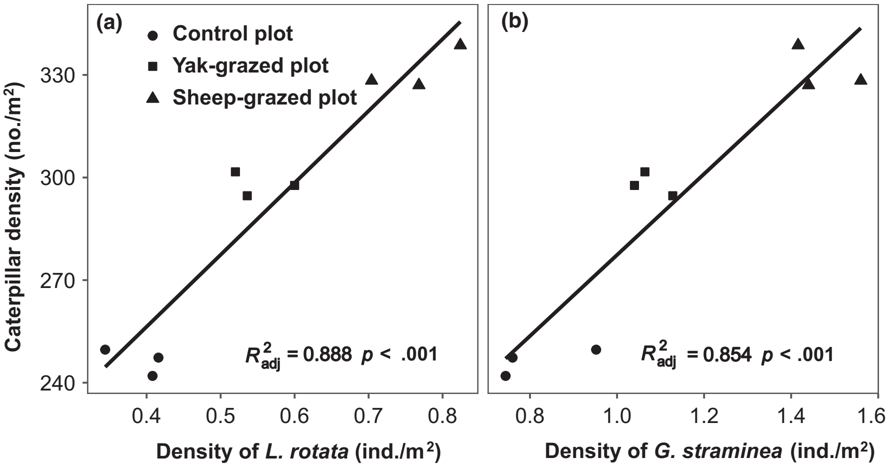

FIGURE 4 Relationship between total density of caterpillars and (a) *Lamiophlomis rotata* and (b) *Gentiana straminea* in the nine plots (six grazed and three ungrazed plots)

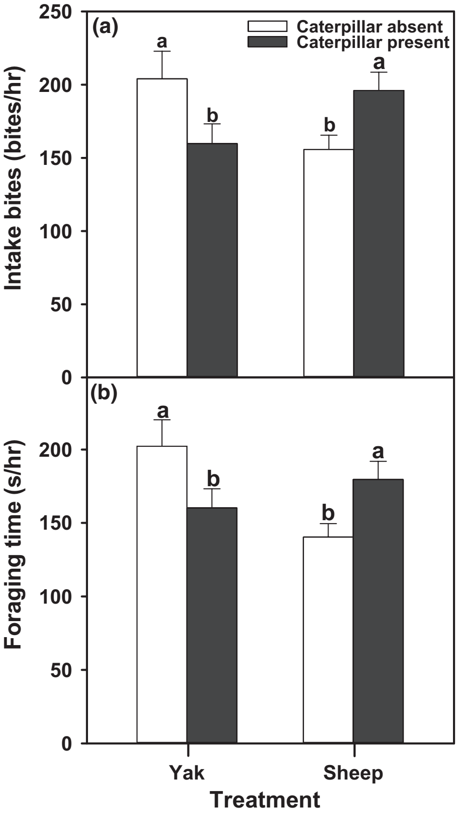

FIGURE 5 Foraging behaviour of large herbivores in caterpillar-absent and present subplots. (a) Total intake bites. (b) Total foraging time. Different letters above the bars indicate significant difference at $p < 0.05$ within each large herbivore grazing treatment. Error bars represent ± *SE*

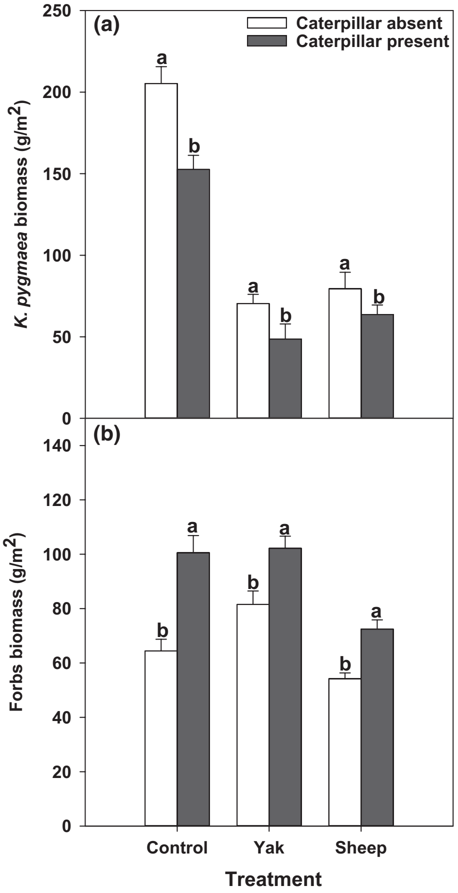

FIGURE 6 Food resources of large herbivores in caterpillar-absent and present subplots. Above-ground biomass of (a) *Kobresia pygmaea* and (b) forbs *Aster flaccidus*, *Polygonum sibiricum* and *Saussure stella*. Different letters above the bars indicate significant difference at $p < .05$ within each large herbivore treatment. Error bars represent ± *SE*

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 (Figure 3b,c). We also found that the densities of the two plant species were significantly and positively related to that of the caterpillars (Figure 4). Therefore, rather than available food resources, we argue that change in habitat was more important in mediating the net effects of large vertebrate herbivores on insect herbivores. Diet selection by caterpillars may also have changed in grazed plots, with positive impacts, but we did not quantify this.

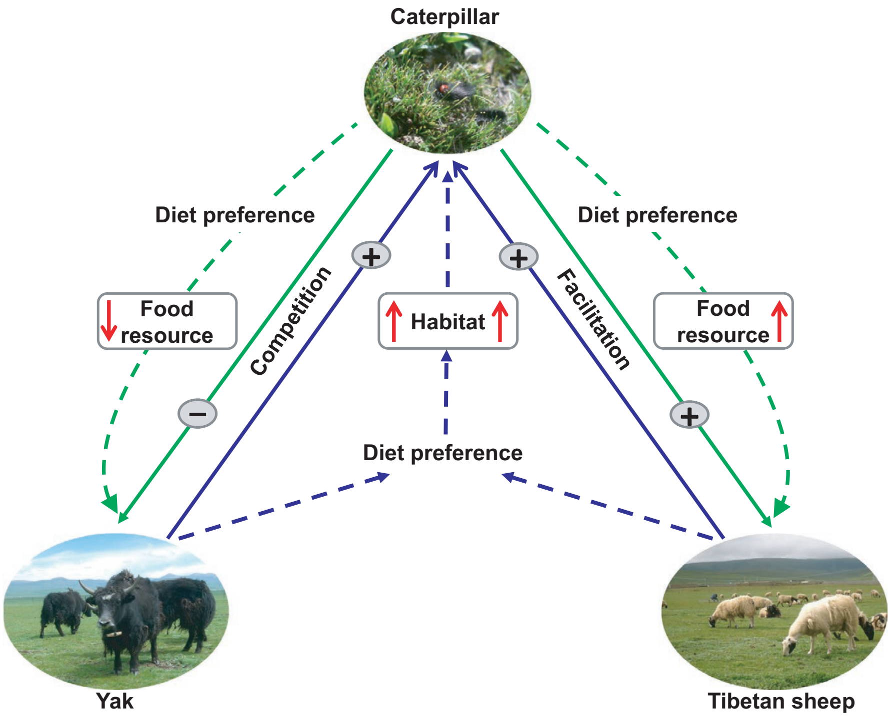

FIGURE 7 A conceptual model showing the reciprocal interactions between caterpillars and yak or Tibetan sheep by changing food resources or habitat structure based on their diet preferences. The + and − symbols indicate positive and negative effects, respectively. The upwards and downwards (red) arrows 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

There are also some other potential mechanisms that could be important in explaining 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 benefit small herbivores sharing the same plant (Bakker et al., 2009; van Klink, van der Plas, van Noordwijk, WallisDeVries, & Olff, 2015). Large herbivores may also facilitate insect herbivores by breaking down the associational plant defences, making the host plant more susceptible to insect herbivores (Frenette-Dussault, Shipley, & Hingrat, 2013; 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. In summary, while negative effects of larger herbivores on smaller ones may be common (Foster, Barton, Lindenmayer, & Toit, 2014; Takagi & Miyashita, 2014), our results suggest that the facilitation between distant related herbivores may be prevalent in some ecological communities.

4.2 | Effects of insect herbivores on vertebrate herbivores

As expected, the caterpillars reduced the biomass of the dominant species, *K. pygmaea* (Figure 6a), the main food resource for yak and caterpillars, thus negatively affecting yak foraging. Nevertheless, caterpillar 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. Additionally, herbivorous insects can induce secondary growth on their host plants, making more nutritious, new-growth tissues available to other herbivores (Utsumi & Ohgushi, 2008). However, we are not sure whether insect herbivore 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. The declining of biodiversity provision, carbon sequestration, water retention and pastoral production caused by grassland degradation have been negatively affected not only the local pastoralists but also the ecological safety (Dong et al., 2015). 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, for example 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.

5 | 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: in this study system, large herbivores affected small herbivore insects mainly through modifying habitat structure and small herbivore insects affected larger herbivores by changing their food quantity (Figure 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.

ACKNOWLEDGMENTS

We thank Jie Li and Peijie Ma for assisting the field work. This project was supported by National Natural Science Foundation of China (Numbers 31772652, 31770520), the Program for Introducing Talents to Universities (B16011), the National Key Research and Development Program of China (2016YFC0500602) and the Ministry of Education Innovation Team Development Plan (2013-373).

AUTHORS' CONTRIBUTIONS

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

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.g01j27q (Pan et al., 2019).

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How to cite this article: Pan D, Li X, De K, et al. Food and habitat provisions jointly determine competitive and facilitative interactions among distantly related herbivores. *Funct Ecol*. 2019;00:1–10. https://doi.org/10.1111/1365-2435.13456