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RESEARCH ARTICLE

Interspecific interactions between burrowing dung beetles and earthworms on yak dung removal and herbage growth in an alpine meadow

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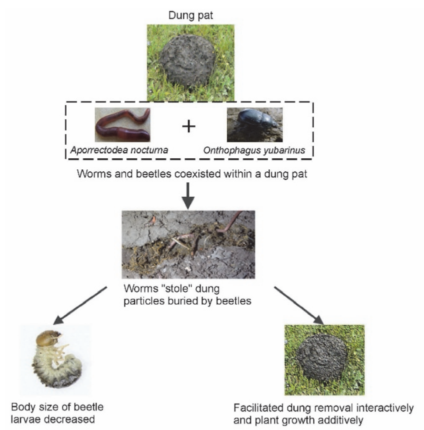
HIGHLIGHTS

• A one-sided negative relationship existed between tunneling beetles and earthworms.
• Beetles and earthworms interactively increased dung removal.
• Beetles and earthworms additively facilitated plant growth.

GRAPHICAL ABSTRACT



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ABSTRACT

Interspecific interactions between two spatiotemporally co-occurred species sharing a single resource are considered to be either competitive or facilitative. This study examined the possible interspecific interactions between a dung-tunneling beetle species (*Onthophagus yubarinus*) and an earthworm species (*Aporrectodea nocturna*), two major detritivores responsible for dung removal in a Tibetan alpine meadow. We conducted a two-way, factorial field experiment using replicated chambers, and measured the performances of beetles and earthworms, as well as yak dung removal, soil properties and aboveground plant biomass over two months. Earthworm presence significantly decreased the body size of beetle larvae and the weight of tunnel dung that beetle larvae live on. In contrast, beetle presence did not affect the performance of earthworms. Beetles, earthworms and their interaction significantly increased dung removal and soil organic carbon concentration at the end of the experiment. Beetles alone significantly increased soil total N and P, soluble N and P concentrations, but earthworms alone had nonsignificant effects on these nutrient variables. Beetles and earthworms additively enhanced soluble N and P concentrations, and aboveground plant biomass at the end of the experiment. These results indicate 1) there was a one-sided negative relationship between dung-tunneling beetles and earthworms, resulting from the consumption of earthworms on food resource of beetle larvae; and 2) the coexistence of beetles and earthworms facilitated dung removal interactively and plant growth additively by increasing nutrient availability.

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1 Introduction

Examining the potential of interspecific interactions between closely related species sharing a single resource is a long-standing topic in community ecology (Gause, 1934; Denno et al., 1995; Bird et al., 2019). Relative to the extensive examination on interspecific interactions among herbivorous species and its importance in structuring communities (Denno et al., 1995; Bird et al., 2019), interspecific interactions among organisms in detrital systems are seldom explored. This probably reflects the fact that the classic theories of interspecific interactions have traditionally focused on living organisms but have neglected detritus since the development of classical community ecology and ecosystem ecology in the 1950s (Moore et al., 2004). It may also be because the fact that compared with herbivores, detritivores are more diverse but are less identified (Gessner et al., 2010).

Soil macrofauna play important roles in controlling soil structure dynamics and regulating ecosystem functions (Gessner et al., 2010; Bottinelli et al., 2015; Chen et al. 2020). Some macro-invertebrate groups such as earthworms, termites and ants, known as “soil engineers” (Jones et al., 1994; Gessner et al., 2010), have ability to burrow and create nest structures in soil, largely influencing the physical environment where they live and importantly, these groups can also transport and incorporate soil surface organic matters into the soil profile. Consequently, their burrowing and foraging activities largely change soil physicochemical properties and the corresponding regulation of soil ecological functions and ecosystem services (Lavelle et al., 2006; Huhta, 2007).

Dung is an important source of organic matter in many grazing pastures (Mohr, 1943; Yamada et al., 2007; Wu and Sun, 2010; Holter, 2016), because most of plant biomass in these systems consumed by livestock is not assimilated but released as droppings (Chew, 1974). The deposition of dung and its subsequent decomposition has been shown to affect soil physical properties (Brown et al., 2010; Wu et al., 2014), nutrient cycling (Wu et al., 2011; Yamada et al., 2007) and plant primary productivity (Nichols et al., 2008).

Decomposition of dung has been demonstrated to depend largely on invertebrate detritivores (Mohr, 1943), some of which are soil engineers including earthworms in temperate and trophic pastures (Holter, 1977, 1979; Scown and Baker, 2006), termites in arid and semi-arid regions (White, 1960; Freymann et al., 2008) and tunneling beetles in Mediterranean and highland grasslands (Lumaret et al., 1992; Wu et al., 2014). Importantly, these detritivore groups such as tunneling beetles and earthworms may coexist within a dung pat (e.g., Holter, 1977; Zhao et al., 2013). Tunneling beetles bury dung in tunnels excavated beneath dung pats that range from several to dozens of centimeters in depth depending on the species and soil conditions (Edwards and Aschenborn, 1987; Sowig, 1995; Wu et al., 2014). The dung is utilized as a medium for feeding and breeding. Beetle adults make dung into a ball, transport it in a chamber at the end of the tunnel and lay an egg in the ball. Beetle larvae eat the dung ball and remain in the soil from months to years before emerging as adults (Halffter and Edmonds, 1982). Correspondingly, earthworms can also burrow, transport and combine dung with soil. Previous literatures have suggested that tunneling beetles and earthworms are separately able to change soil physical and chemical conditions, mediate decomposition of organic material, and facilitate plant growth (Lumaret et al., 1992; Scown and Baker, 2006; Wu et al., 2014). However, relationships between them and their interaction on ecosystem functions when they coexist have never been examined. The current study was thus designed to 1) determine to how and what extent of tunneling beetles and earthworms influenced each other, 2) test whether their interaction influenced the removal of cattle dung and plant growth.

2 Material and methods

2.1 Study site and natural history

Our study was conducted in an alpine meadow in Hongyuan County (32°48′N, 102°33′E), in the eastern part of the Qinghai-Tibetan Plateau. Further details of the climate and plant community can be found in the previous studies (Wu et al., 2014, 2019).

In the study meadow, yaks (*Bos grunniens*) are the main grazing livestock (Xiang et al., 2009), and the density of yak dung pats is very high, with the highest recorded value of 5900 pats per hectare (Wu and Sun, 2010). The decomposer community within dung pats includes a diverse detritivore assemblage, including beetles, flies, ants, earthworms, and their associated predators (e.g., spiders, centipedes, and predatory beetles; Wu and Sun, 2010). Coprophagous beetles are the most effective detritivores (Wu and Sun, 2010). According to feeding behaviors, coprophagous beetles are usually classified into four species groups (Doube, 1990): tunnellers (paracoprids) that dig tunnels beneath dung pats and transport dung balls into the tunnels for feeding and breeding; dwellers (endocoprids) that feed and breed within dung pats; rollers (telecoprids) that roll dung balls away from dung pats and store them for feeding and breeding; and kleptoparasites (kleptocoprids) that use dung balls stored by tunnellers or rollers. In our study area, the two most abundant beetle groups are dwellers including *Aphodius erraticus*, *A. rectus*, *A. rusicola*, *A. edgardi*, *A. frater*, and tunnellers including *Onthophagus yubarinus*, *O. tabidus*, *Germarostes* sp. Of which, *Onthophagus yubarinus* (15.1–19.4 mm in adult body length) accounting for about 10% (averagely eight adult individuals per pat) of the total number of coprophagous beetles, is active from June to September in dung pats. This species can significantly affect dung removal, soil properties and the associated plant growth (Wu et al., 2014). In addition, two earthworm species, *Aporrectodea nocturna* (about 5 cm and 3 mm in adult body length and diameter, respectively) and *Pheretima aspergillum* (>10 and 0.5 cm in length and

Fig. 1 Earthworms occupied the tunnel burrowed by beetles (left) and destroyed the dung ball stored by beetles (right). Photo by X. Wu.

diameter, respectively), are known to be active in the study region (Zhao et al., 2013). Both earthworm species are found within or underneath dung pats (Fig. 1) with a high density, particularly for *A. nocturna* (averagely 20 individuals but can reach 80 individuals per pat as the highest recorded; Zhao et al., 2013).

2.2 Experimental design and sampling

We conducted a two-way, full factorial experiment, consisting of four treatments: (1) B–, E– (neither beetles nor earthworms added), (2) B–, E + (beetle absent, earthworm present), (3) B + , E– (beetle present, earthworm absent), and (4) B + , E + (both beetle and earthworms added). Each treatment had 18 replicates. We first randomly selected 72 circular plots, each with a dimeter of 0.5 m and separated by at least 3 m, on May 12 of 2016, in a fenced 0.5 ha pasture. This pasture had a vegetation cover >95%, and thus each plot enclosed most of naturally-occurring plant species. The electro-shocking method was applied to remove pre-existing earthworms (if any) from each plot using self-made stainless-steel probes (6.4 mm in diameter and 30 cm in length) and a portable generator (to generate an electric current ~2 Amps), following Fonte et al. (2007). After adding water to the plot to bring the soil near field capacity, we inserted four evenly spaced probes into soil, removing earthworms for a total of 15 min, after which no more earthworms were found (Zhao et al., 2013). Then, a circular core (30 cm × 20 cm, diameter × depth) of above- and below-ground plant materials and soil was trenched and carefully extracted from the ground in the center of the plot. Because plant roots are usually < 20 cm in depth and are very dense in the meadow, we were able to remove the whole plant-root-soil system intact during coring. Subsequently, cores were transplanted into cylindrical chambers (30 cm × 30 cm, diameter × depth), with siding made of 0.5 mm aluminum sheeting, and a bottom made of a steel screen (0.3 mm thick). The mesh size of the screen was 0.5 mm × 0.5 mm, which prevented beetles and earthworms from escaping and allowed water to drain. Finally, these experimental chambers were placed back into the ground where they were dug out. In addition, the tops of chambers were covered with the same screen as the chamber bottom to prevent beetles or earthworms or other animals from leaving or entering. The light intensity under such screens was about 80% of full sunlight (Zhao et al., 2013).

The experiment began on 11 June and ended on 10 August 2016. When the experiment started, dung was collected in the early morning (before 7:00 am) from fresh droppings by yaks in a stall of a Tibetan family, such that the dung was free of beetles and other macro-decomposers. The dung was thoroughly mixed in big buckets, and then divided into individual pats using a circular metallic mold. The pats were 17 cm in diameter and 1000 g (±25 S.E.) in fresh weight (ca. 5 cm thick). One dung pat was placed on the ground in the center of each chamber. Beetles and earthworms were collected by hand two days before. We selected only the medium-sized individuals of each species (~1.7 cm and 5 cm in length on average for the beetle and worm species, respectively) for the experiment. 20 individuals of *A. nocturna* and 8 (four male and four female) individuals of *O. yubarinus* were added to the chambers according to treatment. The numbers were within the ranges of the field density of beetle and worm populations. After the addition of dung, beetles and worms, we sealed the top of each chamber.

During the course of the experiment, we sampled twice, each time with six replicates for each treatment. The sampling dates were on 21 June (after 10 days since the beginning of experiment) and 11 July (after 30 days). We took out the soil core and then recorded the number of tunnels that the beetles burrowed, and measured the depth of each tunnel; we also collected the dung from the tunnels, which was then dried and weighed as "tunnel dung weight" (i.e., mass of the dung used for the beetle brooding in the tunnels, see Sowig, 1996). In addition, the living beetles and earthworms (including eggs and larvae of both species, if any) within the dung pats, tunnels and soil were also collected and counted and weighted, respectively. But, we did not sample soils and plants for the first two-time samplings.

On 10 August (after 60 days), we conducted the third sampling for the remaining 24 chambers. We did not collect data on the number of tunnels and the tunnel depth and tunnel dung weight because tunnels in soil were undistinguishable after such a long time. Aboveground parts of plants and the remaining dung in each chamber were collected and weighed separately after being dried at 75°C for 48 h. Then, we took out the soil core and manually sieved the soil, counted and weighted worms and beetles (including the living adults and larvae, if any). Notably, on the first sampling time (after 10 days), all the eight beetle adults were living and crawling inside the chamber but not within the dung pat and tunnels. We also did not found any worm eggs and juveniles during the three samplings. Finally, 500 g mixed soil samples were collected. For each soil sample, organic carbon concentration was determined by the potassium dichromate oxidation-outer heating method; total N and P concentrations were determined by the Kjeldahl method and spectrophotometric Colorimetry (Unicam-200, Unicam, Cambridge, UK), respectively; soluble N and P concentrations were determined using the alkaline $KMnO_4$ method and 0.5 M $NaHCO_3$ (pH 8.5) solutions, respectively.

2.3 Data analysis

Kolmogorov–Smirnov and Levene's tests were used to check the normality of the distribution and variance homogeneity of the sample residuals, respectively. Two-way analysis of variance (ANOVA) was employed to determine the effects of beetles, earthworms, and their interaction on soil properties including soil organic carbon, total N and P, soluble N and P concentrations, as well as the residual dung weight and aboveground plant biomass at the end of the experiment. Once a significant effect was detected, the difference between treatments was determined using *post hoc* Tukey tests. A generalist linear mixed model (GLMM with Poisson error), in which presence of earthworms or beetles was set as the fixed factor and sampling date as the random factor, was built to test the differences in tunnel dung weight, tunnel depth and tunnel number as well as the number and body mass of both burrowers between different treatments. All the data analyses were performed in R 3.5.0 (R Core Team, 2018).

3 Results

3.1 Performances of beetles and earthworms

Presence of earthworms persistently and significantly reduced the tunnel dung weight (GLMM: $F_{1,21} = 81.32$, $P < 0.001$; Fig. 2A) and beetle larval size (GLMM: $F_{1,21} = 38.16$, $P < 0.001$; Fig. 3B), but did not affect beetle larval number (GLMM: $F_{1,21} = 0.5$, $P = 0.487$; Fig. 3A), tunnel depth (GLMM: $F_{1,21} = 0.10$, $P = 0.751$; Fig. 2B) and tunnel number (GLMM: $F_{1,21} = 0.06$, $P = 0.811$; Fig. 2C) during the experiment. Conversely, presence of beetles affected neither earthworm number (GLMM: $F_{1,33} = 2.78$, $P = 0.141$; Fig. 3C) nor earthworm size (GLMM: $F_{1,33} = 0.33$, $P = 0.856$; Fig. 3D) during the experiment.

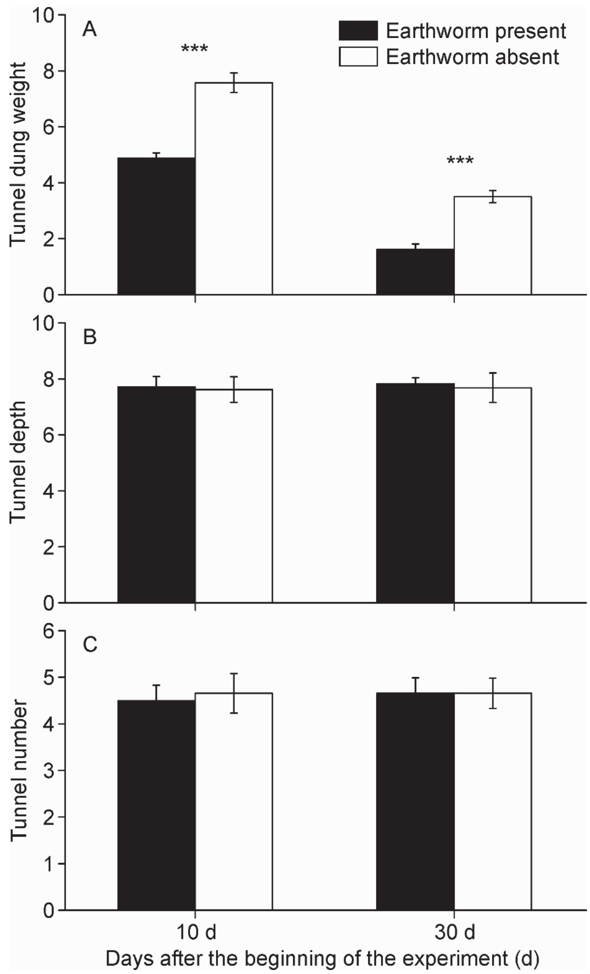

Fig. 2 Tunnel dung weight (A), tunnel depth (B) and tunnel number (C) in the presence and absence of earthworms during the experiment. ***, $P < 0.001$.

3.2 Roles of beetles and earthworms

Beetles and earthworms alone significantly enhanced aboveground plant biomass by 20% and 14% (Table 1; Fig. 4A),

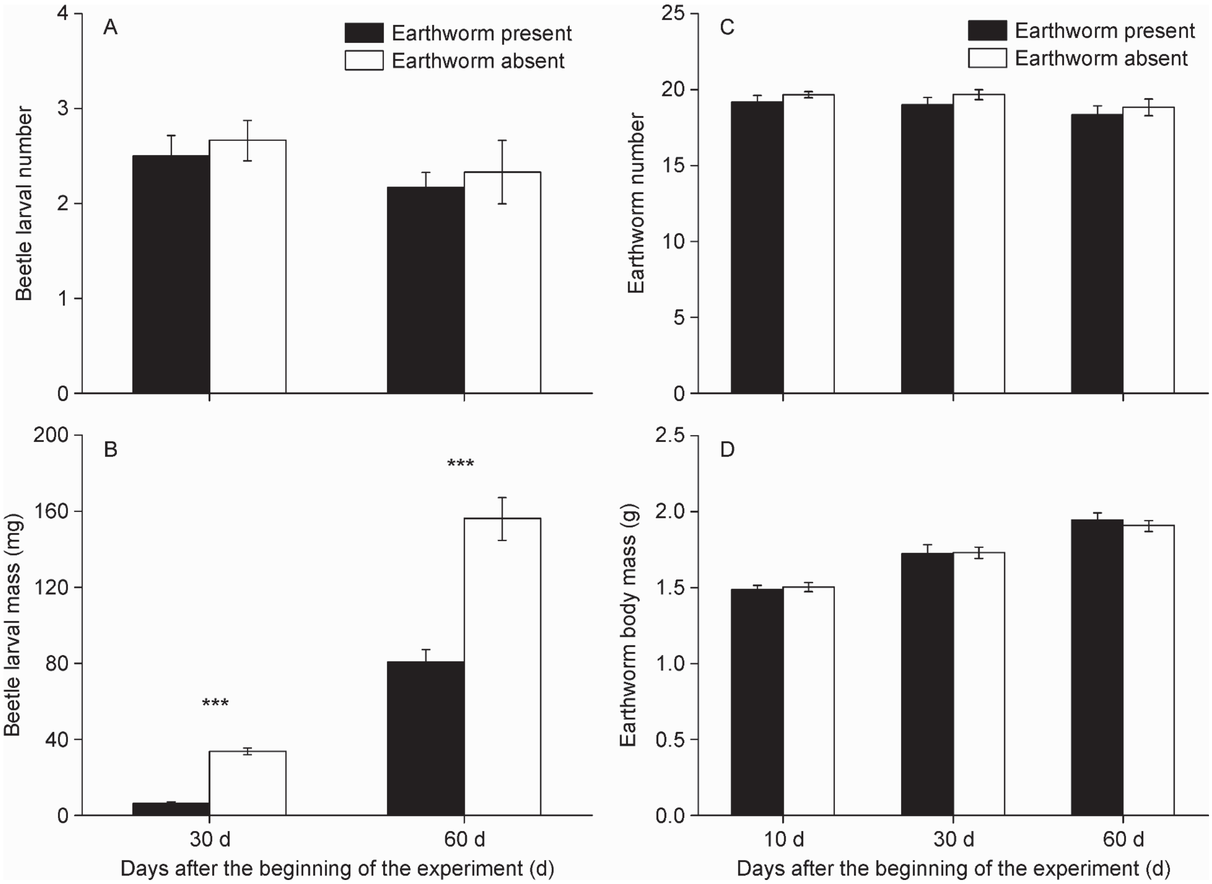

Fig. 3 The number (A) and body mass (B) of beetle larvae in the presence and absence of earthworms, and the number (C) and body mass (D) of earthworms in the presence and absence of beetles during the experiment. ***, $P<0.001$.

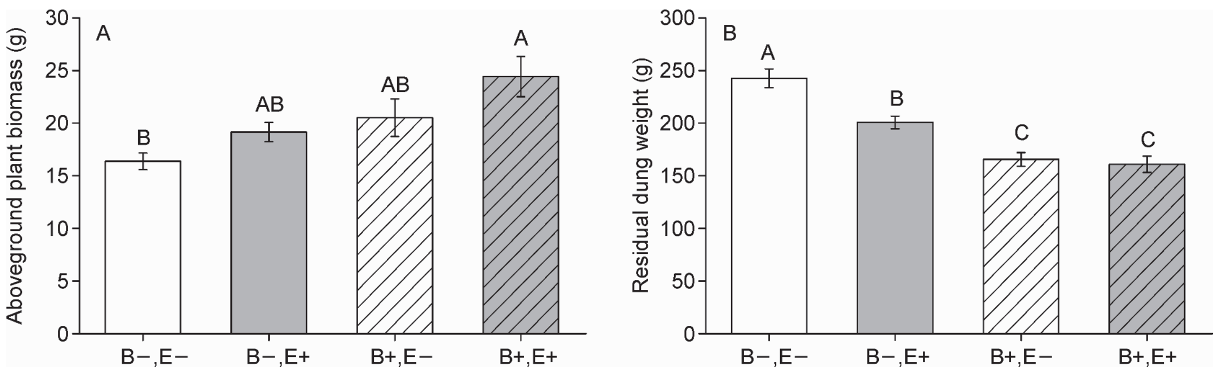

Fig. 4 Variations in aboveground plant biomass (A) and residual dung weight (B) among the four experimental treatments ((1) neither beetles nor earthworms added (B–, E–), (2) beetle absent, earthworm present (B–, E +), (3) beetle present, earthworm absent (B +, E–), and (4) both beetle and earthworms added (B +, E +)) at the end of the experiment. Different letters above the error bars denote statistically significant differences among means ($P=0.05$), as revealed by ANOVAs followed by Tukey's HSD test for multiple comparisons. Sample size was 6 for all the treatments. Means$\pm$standard error.

respectively. Beetles and earthworms additively enhanced plant biomass by 34% (Table 1; Fig. 4A). In addition, beetles and earthworms as well as their interaction significantly reduced dung removal (Table 1; Fig. 4B) at the end of the experiment. Beetles removed 51 mg dung per individual whereas earthworms removed 14 mg per individual over 60 days.

In addition, beetles, earthworms and their interaction significantly enhanced soil organic carbon concentration (Table 1; Fig. 5A). Beetles alone significantly enhanced soil

Table 1 The results of two-way ANOVAs showing the effects of beetles (B), earthworms (E), and their interaction (B*E) on aboveground plant biomass, residual dung, soil organic carbon, soil total N and total P as well as soluble N and P concentrations at the end of the experiment.

		MS	df	SS	F	*P*
Aboveground plant biomass	B	131.84	1	131.84	10.75	0.004
	E	67.03	1	67.03	5.46	0.030
	B*E	1.94	1	1.94	0.16	0.695
	Error	245.37	20	12.27		
Residual dung	B	20570.96	1	20570.96	62.73	< 0.001
	E	3155.17	1	3155.17	9.62	0.006
	B*E	1987.44	1	1987.44	6.06	0.023
	Error	6558.48	20	327.92		
Organic carbon	B	31864.98	1	31864.98	44.80	< 0.001
	E	3480.72	1	3480.72	4.89	0.039
	B*E	8641.49	1	8641.49	12.15	0.002
	Error	14226.81	20	711.34		
Total N	B	17.56	1	17.56	7.07	0.015
	E	3.48	1	3.48	1.40	0.251
	B*E	12.04	1	12.04	4.84	0.040
	Error	49.70	20	2.48		
Total P	B	0.06	1	0.06	8.53	0.008
	E	0.01	1	0.01	1.74	0.202
	B*E	0.00	1	0.00	0.10	0.753
	Error	0.14	20	0.01		
Soluble N	B	786209.70	1	786209.70	75.40	< 0.001
	E	32955.98	1	32955.98	3.16	0.091
	B*E	7835.51	1	7835.51	0.75	0.396
	Error	208553.86	20	10427.69		
Soluble P	B	1259.50	1	1259.50	18.17	< 0.001
	E	39.08	1	39.08	0.56	0.462
	B*E	0.44	1	0.44	0.01	0.937
	Error	1386.43	20	69.32		

total N (Table 1; Fig. 5B) and P (Table 1; Fig. 5C), soluble N (Table 1; Fig. 5D) and P (Table 1; Fig. 5E) concentrations. Earthworms alone had nonsignificant effects on these nutrient variables (Table 1; Fig. 5B-E). Beetles and earthworms additively enhanced soluble N (Table 1; Fig. 5D) and P (Table 1; Fig. 5E) but not soil total N (Table 1; Fig. 5B) and P (Table 1; Fig. 5C) at the end of the experiment.

4 Discussion

The interspecific relationship between two co-occurred species sharing a single resource has largely been demonstrated to be either competitive or facilitative in the living plant-based ecosystem (Denno et al., 1995; Reitz and Trumble, 2002). More than 40 years ago, in a dung-based detrital system, Holter (1977) reported that there was an additive but not interactive effect between beetle larvae (i.e., *Aphodius* larvae) and earthworms on dung removal. Notably, however, the beetles Holter used were a dung-dwelling species that feed and breed within the dung pat. In this present study, the observed one-sided negative relationship between dung-tunneling beetles and earthworms further validates the prediction that interspecific interactions between detritivore species are context-dependent (Wu et al., 2015; Slade and Roslin, 2016). The strong negative effect of earthworm interference on beetles appears to be largely due to the fact

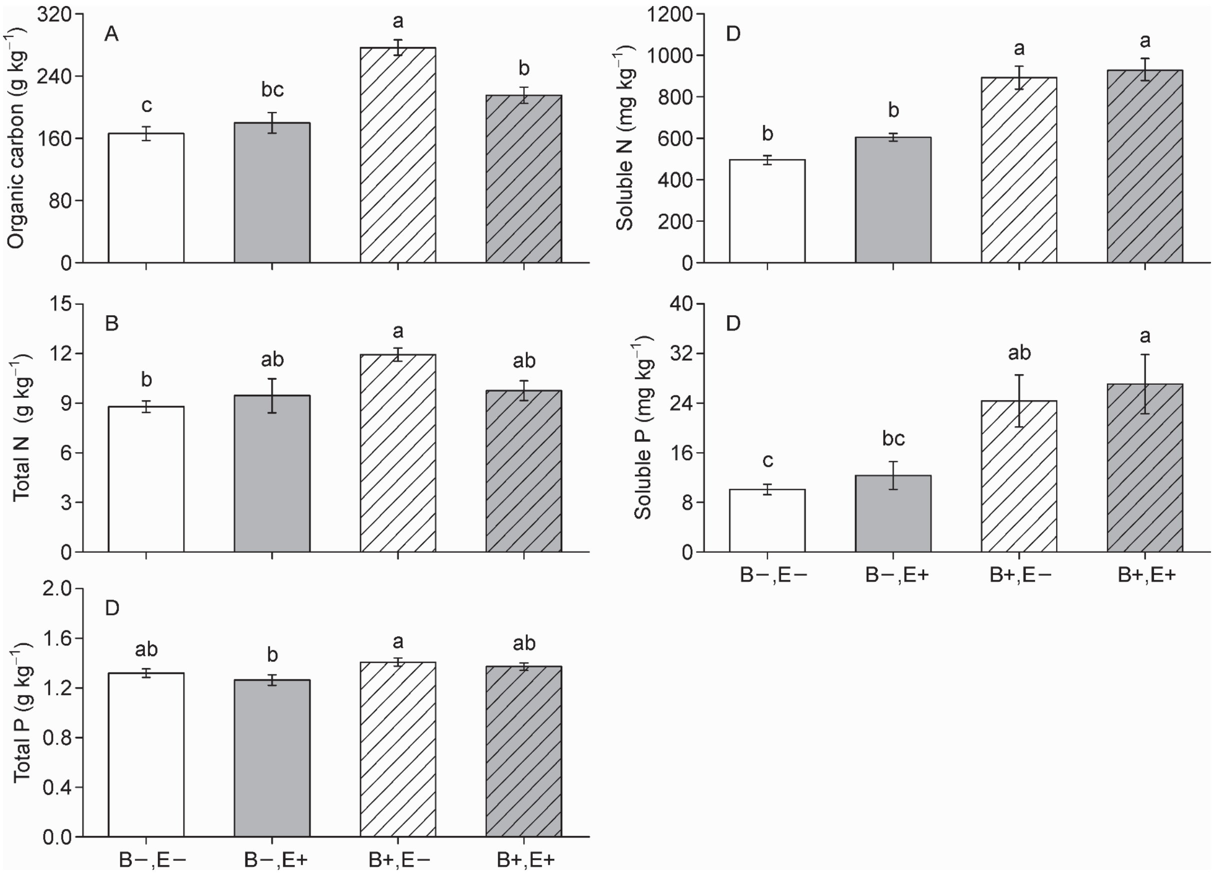

Fig. 5 Variations in soil organic cabon (A), soil total N (B) and P (C), soil soluble N (D) and P (E) concentrations among the four experimental treatments ((1) neither beetles nor earthworms added (B–, E–), (2) beetle absent, earthworm present (B–, E+), (3) beetle present, earthworm absent (B+, E–), and (4) both beetle and earthworms added (B+, E+)) at the end of the experiment. Different letters above the error bars denote statistically significant differences among means (P = 0.05), as revealed by ANOVAs followed by Tukey's HSD test for multiple comparisons. Sample size was 6 for all the treatments. Means±standard error.

that earthworms reduced the food resource of beetle larvae, i.e., tunnel dung. Within coprophagous Scarabaeid beetles, tunnellers are the only group evolved the brood care behavior (Sowig, 1995), i.e., beetle parents store dung balls in soil tunnels beneath the dung pat for their offspring. Meanwhile, some earthworm species including *Aporrectodea nocturna* in our study area have been reported to prefer dung than soil (Scown and Baker, 2006). Earthworms not only ate dung in the tunnel, but their activity also disrupted the dung ball that beetle larvae lived in (Fig. 1). Nevertheless, earthworms did not affect the tunneling behavior of beetle adults, as reflected by the changeless tunnel number and tunnel depth. In addition, we did not find any benefits for the earthworm population resulted from this "steal" behavior.

Both beetles and earthworms significantly contributed to dung removal, and beetles were found to remove more dung than earthworms. One important reason for this may be that beetle adults transported and stored amounts of dung for their larvae in addition to feeding themselves. Importantly, more dung removed by beetles to the soil directly resulted in higher soil organic carbon and soil total N and P concentrations because yak dung contains high proportion of organic matter and nutrients (Wu and Sun, 2010). In addition, the burrowing activities of both beetles and earthworms may have greatly improved soil conditions. There is good evidence that tunnels can make a significant contribution to soil aeration by increasing the porosity and the air-to-soil volume (Edwards and Lofty, 1977). Tunnels can also improve soil drainage and nutrient leaching from the topsoil layer and dung pats, particularly for beetles that can penetrate vertically deep into the soil (Wu et al., 2015). Moreover, the digestion activities of beetles and their larvae as well as earthworms, together with improved soil aeration, might have improved microbial activity (Slade et al., 2016), contributing to the increased levels of soluble nutrients (although statistically nonsignificant for earthworms) in the soil. Consequently, these improvements in soil conditions probably facilitated nutrient uptake by roots, ultimately increasing aboveground plant biomass.

When beetles and earthworms coexisted, earthworms "stole" part of dung within tunnels burrowed by beetles, that is to say, earthworms themselves removed less dung in the presence of beetles. This can largely explain the negative interactions between beetles and earthworms on dung removal and soil organic carbon. Given that earthworms and beetles did not influence the burrowing behavior of each other, it is reasonable to speculate that they additively improved soil conditions. Consequently, earthworms and beetles additively enhanced soil nutrient availability and the associated aboveground plant biomass.

5 Conclusions

We here found that presence of earthworms significantly and negatively affected beetle larval size whereas beetles did not affect the performance of earthworms, which indicates that there was a strong one-sided negative relationship between tunneling beetles and earthworms. Importantly, the coexistence of beetles and earthworms facilitated dung removal interactively as well as nutrient availability and the associated aboveground plant biomass additively. Considering the presence of large and steadily increasing populations of grazing animals in the Qinghai-Tibetan meadows, and the species and functional diversity of dung detritivores, our findings are important to understanding the interspecific interactions among dung detritivores and its role in regulating ecosystem functions.

Conflicts of interest

All authors declare that they have no conflict of interest.

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