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Plateau pika disturbances alter plant productivity and soil nutrients in alpine meadows of the Qinghai-Tibetan Plateau, China

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Abstract. Plateau pika (*Ochotona curzoniae*) is an endemic mammal in the Qinghai-Tibetan Plateau, and its activities create extensive disturbances on vegetation and soil of alpine meadow. Field surveys at two sites were conducted to determine the effects of plateau pika disturbances on important soil factors and plant biomass of vegetated land, and their relationships of the same alpine meadow type. Our study showed that plateau pika disturbances significantly increased soil organic carbon, soil total nitrogen, graminoid biomass and the number of plant species, and significantly decreased soil moisture and forb biomass, although they had no significant impacts on soil total phosphorus, soil total potassium and total biomass on vegetated land. Our study further showed that soil organic carbon, soil total nitrogen, graminoid biomass and the number of plant species were much higher at intermediate disturbance intensities than those at low and high disturbance intensities in the disturbed areas, and soil moisture showed a decreasing trend with the increase of disturbance intensity. Plateau pika disturbances altered the contribution of some important soil nutrients and moisture to plant biomass, and had different impact on the best models between plant biomass (total biomass, graminoid biomass and forb biomass) and predominant soil factors. Our results demonstrated that the optimal disturbance intensities of plateau pika were beneficial to alpine meadow. These results highlighted the influence of the presence of plateau pika and its disturbance intensity on key soil nutrients and plant productivity on vegetated land of the same alpine meadow type, which will help us better understand the role of plateau pika in the alpine meadow ecosystem.

Additional keywords: correlation relationship, plateau pika disturbance, plant productivity, soil moisture, soil nutrients.

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Introduction

Rodents often create extensive disturbances on grassland vegetation and soil (Spencer *et al*. 1985; Reichman and Jarvis 1989; Guo *et al*. 2012*a*, 2012*b*; Eldridge and Whitford 2014; Walker *et al*. 2015), which usually change the regional hydrothermal processes in disturbed areas (Li and Zhang 2006; Sun *et al*. 2010; Liu *et al*. 2013*b*), thus ultimately having important impacts on the properties and processes of the ecosystem (Huntly and Inouye 1988; Hagenah and Bennett 2013; Beals *et al*. 2014). Previous studies have shown that rodent disturbances can improve soil nutrients and these improvements vary with the survey regions. However, the improvements of soil nutrients due to rodent disturbances do not always increase plant productivity. Some studies show that rodent disturbances increase nutrient availability in soil while lowering the plant biomass (Hagenah and Bennett 2013; Galiano *et al*. 2014); however, other studies shows that rodents disturbances increase soil total carbon of mounds (Yurkewycz *et al*. 2014), but have no significant effects on plant biomass (Adams *et al*. 2010). Meanwhile, Martínez-Estévez *et al*. (2013) observed that prairie dog disturbances increase the plant biomass.

Plateau pika (*Ochotona curzoniae*), an endemic mammal in the Qinghai-Tibetan Plateau (Guo *et al*. 2012*a*, 2012*b*; Liu *et al*. 2012), is one of the important small rodents found in the alpine meadow ecosystem (Guo *et al*. 2012*a*, 2012*b*). These burrowing animals are social mammals that live in family groups consisting of two to five adults and their young that do not disperse in their year of birth (Smith *et al*. 1986; Dobson *et al*. 1998; Qu *et al*. 2013). Its population density can grow rapidly within a relatively short period, with a peak in early August (Liu *et al*. 1982). Consequently, the Chinese government and local herders have considered this small burrowing rodent a pest (Liu *et al*. 2013*b*), which contributes to alpine grassland degradation (Wilson and Smith 2015) because it competes for forage with livestock and its digging is seen to reduce plant cover and contribute to soil erosion (Guo *et al*. 2012*a*, 2012*b*; Liu *et al*. 2013*b*). Thus, plateau pika has been eradicated by poison to maintain the health of the alpine meadow ecosystem over past decades (Wilson and Smith 2015). However, recent studies argue that plateau pika is a keystone species of the alpine meadow ecosystem (Smith and Foggin 1999; Delibes-Mateos *et al*. 2011) because it can serve as prey for many canids and mustelids (Smith and Foggin 1999), its burrow systems can provide breeding habitats for small birds and lizards (Davidson *et al*. 2008), and its presence increases plant species diversity (Smith and Foggin 1999) and plant biomass in bare patches (Wei *et al*. 2007).

Plateau pika often produces many bare patches that enable alpine meadow to become a mosaic of bare land and vegetated land (land covered with vegetation), which make a good habitat for plateau pika to live because plateau pika prefers to live in an open habitat. Consequently, the impacts of plateau pika disturbances on alpine meadow are not only related to bare land but also related to vegetated land (Guo *et al*. 2012*b*). Even in alpine meadow severely disturbed by plateau pika, the bare land only takes up 22.87% of the surface area (Ma 2006), so most of the area is vegetated land.

There are many experiments studying the soil nutrients of bare land (Wei *et al*. 2006; Xu 2008; Liu *et al*. 2010), however, soil nutrients of vegetated land receive little attention. It is necessary to detect the response of plant biomass and soil nutrients in vegetated land to plateau pika disturbances simultaneously because plant productivity of vegetated land is more than that of bare land, which is helpful to better understand the impacts of plateau pika disturbances on the properties and processes of the alpine meadow ecosystem.

Previous studies ignored alpine meadow types in detecting the influences of plateau pika disturbance on soil and plant productivity (Guo *et al*. 2012*a*, 2012*b*; Liu *et al*. 2013*b*), and this made it difficult to separate whether the impacts are by alpine meadow types or plateau pika disturbance. Therefore, it is better to survey on the same alpine meadow type than different alpine meadow types for investigating the effect of plateau pika disturbance on soil nutrients and plant productivity. Plant biomass of grassland consists of graminoid and forb biomass (Bowman *et al*. 1995; Wang *et al*. 2014), in which the higher ratio of graminoids is the guarantee of grazing quality for alpine meadow (Wang *et al*. 2014). However, how the presence of plateau pika affects the graminoid and forb biomass, and how the relationships between soil nutrients and plant biomass in vegetated land respond to plateau pika disturbances are not well documented. Therefore, the objective of this study is to examine the response of soil nutrients and different plant biomasses (total plant biomass, graminoid biomass and forb biomass) in vegetated land of the same alpine meadow type to plateau pika disturbances, and further examine relationships between important soil factors (including important soil nutrients and soil moisture) and plant biomass through two sites in the Qinghai-Tibetan plateau of China, which can provide useful information for understanding the role of plateau pika and its management in the alpine meadow ecosystem of the Qinghai-Tibetan plateau.

Materials and methods

Site description

This study was conducted simultaneously at Beiluhe Basin in Qinghai province and Gaxiu Basin in Gansu province, China (Fig. 1).

Beiluhe Basin (34°49′N and 92°56′E) is located in a permafrost region with an elevation of 4597 m is one of three regions of stable seasonal snow cover in China where most snowfall occurs in spring and autumn rather than winter (Li and Mi 1983). The climate is plateau continental and the mean annual

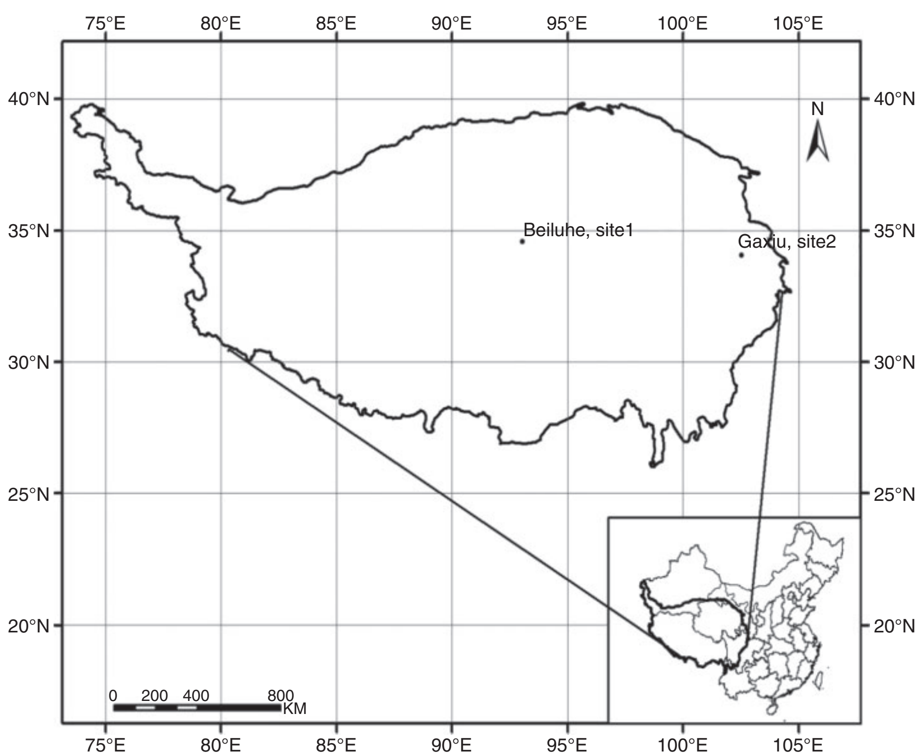

Fig. 1. Locations of the sites on the Qinghai-Tibetan plateau.

temperature is –3.8°C. Annual precipitation is ~290.9 mm and occurs mainly during the period between June and August. The native vegetation is alpine meadow in which the dominant plant is *Carex moorcroftii* and the mainly associate species are *Kobresia pygmaea*, *Poa poophagorum*, *Leontopodinm nanum* and *Oxytropis ochrocephala*.

Gaxiu Basin (34°.26′N and 102°.18′E) is located in a seasonal frozen region and its elevation is 3550 m. The climate is plateau humid with a mean annual temperature of 2.3°C. The average annual precipitation is 633 mm, 56.53% of which occurs from July to September. The native vegetation is alpine meadow in which *Kobresia pygmaea* is the dominant plant, and *Elymus nutans*, *Anemone rivularis*, *Saussurea stella*, *Potentilla anserina*, *P. fragarioides* are other common plants.

Experimental design

Field surveys were carried out in vegetated land at the two sites during 2014. The alpine meadows in the study areas were grazed by yak and have been fenced since 2010 due to the policy of grazing grassland fencing, which encourages the grassland to recover its productivity and ecological function (Gong *et al*. 2012). At each site, we chose the disturbed area where the fresh burrow entrances and plateau pika themselves were simultaneously found, similar to the prairie dogs study by Barth *et al*. (2014) and the badger and fox study by Kurek *et al*. (2014), and the undisturbed area where both fresh burrow entrances and plateau pikas themselves had not been found in early May. Alpine meadow type and topography were remarkably similar between the disturbed areas and undisturbed areas at each site because the disturbed area and the undisturbed area shared the same dominant plants. However, the dominance degree of the dominant plant in the disturbed area declined when compared with the undisturbed area, contributing to a difference in plant height and composition. The distance between the disturbed area and the undisturbed area was ~5 km in Beiluhe Basin and 4 km in Gaxiu Basin, respectively.

The soil types in the disturbed and undisturbed areas were subalpine meadow soil with clay loam texture at Gaxiu Basin, and in the disturbed area and the undisturbed area were alpine meadow soil with clay texture at Beiluhe Basin, according to the Chinese soil classification system. Eight plots with the size of 25 m × 25 m were randomly selected in the disturbed and undisturbed areas respectively, and the distance between plots was over 25 m. Thus, this study consisted of 32 plots (16 plots per site). In late July, the active burrow entrances per plot were recorded by closing burrow entrances for 3 days in disturbed areas at each site (Guo *et al*. 2012*a*, 2012*b*), and the mean value of open burrow entrances over the 3 days of a certain plot was considered the active burrow entrances of that plot.

To assess the effects of disturbance intensities of plateau pika on plant productivity and soil nutrients, the active burrow entrances per plot, with the size of 625 m^2, was used as an index for disturbance intensity of plateau pika (Bagchi *et al*. 2006). The higher active burrow entrances per plot meant the higher disturbance intensity of plateau pika (Guo *et al*. 2012*a*).

Data collection

In July 2014, five sampling subplots with the size of 1 m × 1 m (1 m^2) were designed with a ‘W’ distribution pattern to collect the data in each plot, where the distance between subplots was over 8 m. In the disturbed areas, subplots were designed on vegetated land rather than bare land. All the plant species were identified and recorded in each subplot, and then aboveground materials of all plants in each subplot were harvested by clipping at ground level to determine the plant biomass. The plant samples (160 samples in total) were carried back to the laboratory, and divided into graminoid and forb plants, and dried in an oven at 80°C for 48 h and weighed as graminoid biomass (GB) and forb biomass (FB), the total biomass (TB) was the sum of FB and TB.

After sampling plants, a soil sample was taken from each subplot to a 20-cm depth using a cylindrical metal core sampler with a 5-cm diameter, and the soil moistures (SM) at 10- and 20-cm depths were measured by Time Domain Reflectmetry and their mean values were considered as the soil moisture at 0–20 cm. At the same time, soil samples at the 0–20-cm layer were collected to analyse soil organic carbon (SOC), total nitrogen (STN), total phosphorus (STP) and total potassium (STK). There were 160 soil samples in total and these were carried back to the laboratory. In the laboratory, we removed the vegetative debris, visible roots, stones and soil animals (dead or alive) of 160 soil samples, and soil samples were air-dried at room temperature and sieved to pass a 2-mm screen for measuring soil nutrients. STN was measured by the Kjeldahl procedure (Foss Kjeltec 8400, FOSS, Denmark) (Nelson and Sommers 1982), SOC was determined using the Walkley–Black method (Nelson and Sommers 1982), STP was estimated by Mo-Sb colourimetry (UV-2102C, UNICO, Shanghai, China) and STK was determined by flame photometry (Model 2655-00 Digital Flame Analyser, Cole-Parmer Instrument Co., Chicago, IL, USA) after perchloric and nitric acid digestion in the laboratory (Nelson and Sommers 1982).

Data analyses

The data from five subplots within each plot were pooled to test for differences in the number of plant species, FB, GB, TB, SOC, STN, STP, STK and SM between the disturbed area ($n = 8$) and the undisturbed area ($n = 8$) at each site by non-parametric Wilcoxon-Mann–Whitney test, because ‘disturbed’ and ‘undisturbed’ were regarded as two independent samples in our study. If one of the abovementioned parameters was significantly different between the disturbed and undisturbed areas, the variation trends of this parameter in the disturbed area were further analysed by linear model, in which the active burrow entrance densities were considered as the fixed factor. In order to select the final regression models, which indicated the effect of active burrow entrance densities on soil nutrient and soil moisture, the likelihood ratio tests were used to compare the simple linear regression and polynomial regression models ($n = 8$). The statistical analyses were performed with R version 3.2.3 (R Development Core Team).

Stepwise multiple regression analysis was used to determine the contribution of soil nutrients and soil moisture to plant biomass (TB, GB, FB) in the disturbed area ($n = 40$) and the undisturbed area ($n = 40$). According to R, R^2 and standard error from Stepwise multiple regression equations, the predominant soil factors for plant biomass (TB, GB, FB) were selected in disturbed and undisturbed areas respectively. The selected predominant soil factors were used to establish the best model equations between plant biomass (TB, GB, FB) and soil factors (SOC, STN, STP, STK and SM). Stepwise multiple regression analysis was performed using SPSS 17.0.

Results

Effects of plateau pika disturbances on soil moisture and soil nutrients

The effects of plateau pika disturbances on SM and soil nutrient contents were similar at two sites (Table 1), plateau pika disturbances significantly decreased the SM content ($P < 0.05$), and significantly increased SOC and STN contents ($P < 0.05$), although they had no impacts on STP and STK contents on vegetated land.

In disturbed areas, SM, SOC and STN were strongly influenced by the plateau pika disturbance intensity (Figs 2, 3, 4). With the increase of disturbance intensity, SM showed a decreasing trend (Fig. 2), whereas SOC and STN showed a significantly unimodal curvilinear trends in both sites (Figs 3, 4), in which SOC and STN were much higher at intermediate disturbance intensities on vegetated land.

Table 1. Effects of plateau pika disturbances on soil moisture and nutrients contents (median ± median absolute deviation)

Significant differences between disturbed-undisturbed were tested using a non-parametric Wilcoxon-Mann–Whitney test. Significant differences at *P*-values (<0.05) are in bold. SM, content of soil moisture; SOC, content of soil organic carbon; STN, content of soil total nitrogen; STP, content of soil total phosphorus; STK, content of soil total potassium

Survey sites	Source of variation	Undisturbed ($n = 8$)	Disturbed ($n = 8$)	*P* level
Beiluhe	SM (%)	29.40 ± 5.41	21.50 ± 3.37	**0.006**
	SOC (g/kg)	12.13 ± 2.33	19.19 ± 2.10	**0.001**
	STN (g/kg)	1.41 ± 0.07	1.69 ± 0.12	**0.002**
	STP (g/kg)	0.21 ± 0.02	0.27 ± 0.16	0.529
	STK (g/kg)	2.93 ± 0.93	2.62 ± 0.58	0.833
Gaxiu	SM (%)	16.98 ± 1.70	12.28 ± 1.78	**0.036**
	SOC (g/kg)	38.57 ± 8.21	46.28 ± 6.20	**0.036**
	STN (g/kg)	1.99 ± 0.12	2.87 ± 0.39	**0.001**
	STP (g/kg)	0.61 ± 0.03	0.56 ± 0.09	0.401
	STK (g/kg)	3.18 ± 0.19	3.37 ± 0.08	0.399

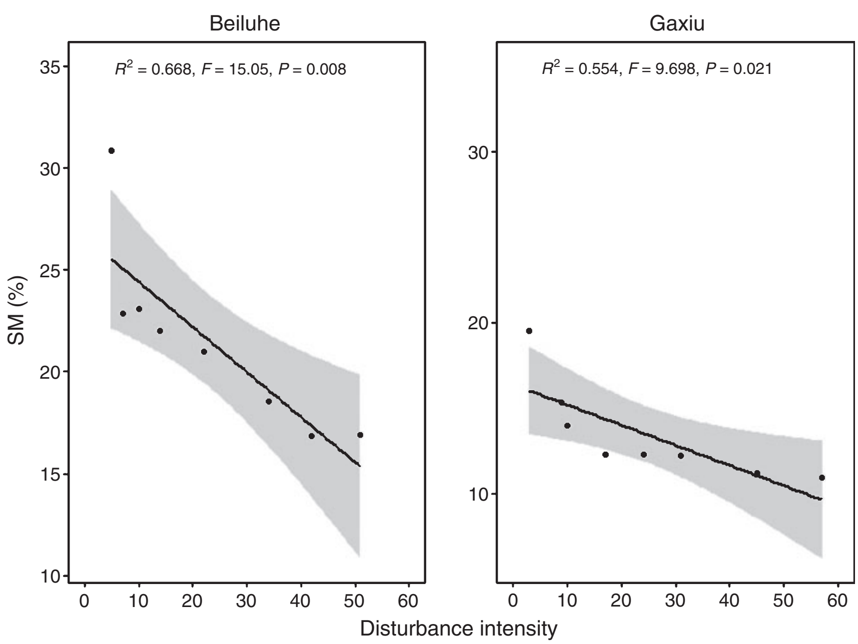

Fig. 2. Mean soil moisture (in %) content (median ± median absolute deviation) in disturbed areas under different disturbance intensity of plateau pika at Beiluhe Basin ($Y = -0.221X + 26.633$. Y, soil moisture. X, disturbance intensity) and Gaxiu Basin ($Y = -0.118X + 16.362$. Y, soil moisture. X, disturbance intensity) based on linear model. For detailed visualisation of the relationship between disturbance intensity and SM, an adjusted local smoothed regression line (black) with its 95% confident interval (grey) was used. Disturbance intensity, active burrow entrances per plot. SM, soil moisture.

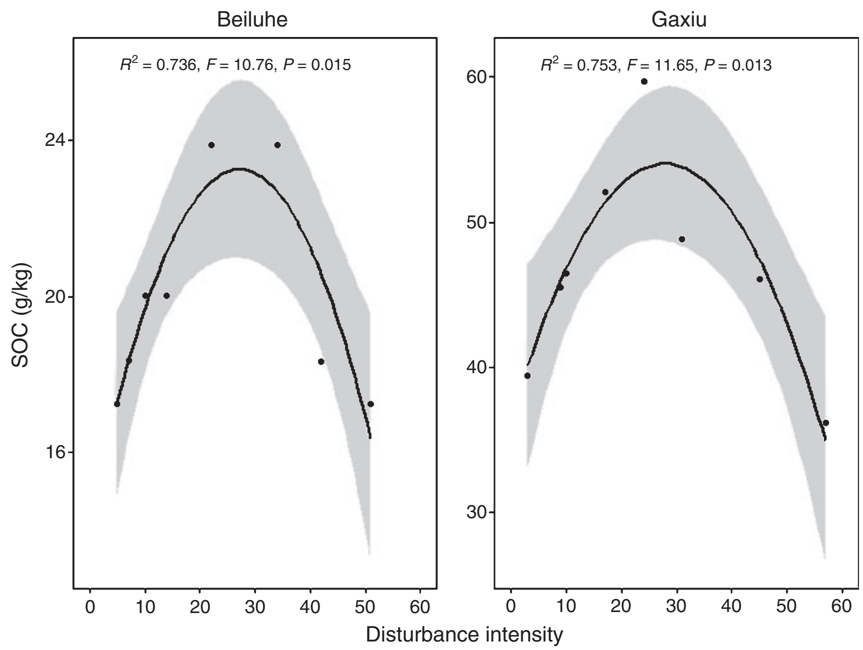

Fig. 3. SOC content (median ± median absolute deviation) in disturbed areas under the different disturbance intensities of plateau pika at Beiluhe Basin ($Y = -0.012X^2 + 0.662X + 14.274$. *Y*, SOC; *X*, disturbance intensity) and Gaxiu Basin ($Y = -0.022X^2 + 1.250X + 36.604$. *Y*, SOC; *X*, disturbance intensity) based on linear model. For detailed visualisation of the relationship between disturbance intensity and SOC, an adjusted local smoothed regression line (black) with its 95% confident interval (grey) was used. Disturbance intensity, active burrow entrances per plot. SOC, soil organic carbon.

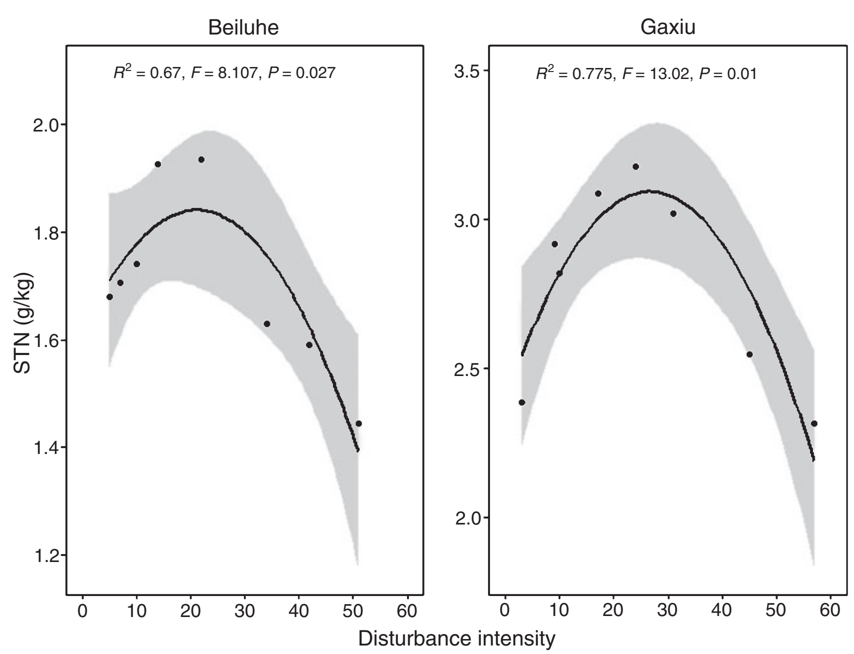

Fig. 4. STN content (median ± median absolute deviation) in disturbed areas under the different disturbance intensity of plateau pika at Beiluhe Basin ($Y = -0.001X^2 + 0.021X + 1.615$. *Y*, STN; *X*, disturbance intensity) and Gaxiu Basin ($Y = -0.001X^2 + 0.052X + 1.396$. *Y*, STN. *X*, disturbance intensity) based on linear model. For detailed visualisation of the relationship between disturbance intensity and STN, an adjusted local smoothed regression line (black) with its 95% confident interval (grey) was used. Disturbance intensity, active burrow entrances per plot. STN, soil total nitrogen.

Effects of plateau pika disturbances on plant species and plant biomass

The number of plant species in disturbed areas was significantly greater than that in undisturbed areas at two sites ($P < 0.05$) (Table 2). Some plant species only occurred in disturbed areas whereas they were absent in undisturbed areas, such as *Sanguisorba arenaria*, *Melissilus ruthenicus* and *Artemisia frigida* in the Beiluhe Basin, and *Oxytropis ochrocephala*, *Astragalus nivalis*, *Lespedeza davurica*, *Plantago asiatica* and *Euphrasia pectinata* in the Gaxiu Basin (Appendix 1). In disturbed areas, the unimodal curve distribution pattern of the number of plant species was observed as the disturbance intensities of plateau pika increased (Fig. 5), and these indicated that the number of plant species in disturbed areas was higher at intermediate disturbance intensities.

The response of plant biomass to plateau pika disturbances was found to be similar in two sites. There were significantly lower FB and significantly higher GB in disturbed areas than those in undisturbed areas (Table 2), although TB was not significantly different between disturbed areas and undisturbed areas in two sites. In disturbed areas, GB presented a first increasing and then decreasing trend with the increase of disturbance intensity (Fig. 6), and was higher at intermediate disturbance intensities, whereas FB was not

Table 2. Effects of plateau pika disturbances on the number of plant species and plant biomass (median ± median absolute deviation)

Significant differences between disturbed-undisturbed were tested using a non-parametric Wilcoxon-Mann–Whitney test. Significant differences at *P*-values (<0.05) are in bold. TB, total plant biomass; GB, graminoid plant biomass; FB, forb plant biomass

Sites	Source of variation	Undisturbed ($n = 8$)	Disturbed ($n = 8$)	*P* level
Beiluhe	TB (g/m^2)	32.43 ± 13.31	30.20 ± 7.99	0.916
	GB (g/m^2)	17.24 ± 3.66	23.62 ± 3.92	**0.036**
	FB (g/m^2)	14.01 ± 4.58	8.46 ± 1.70	**0.036**
	Plant species richness	7.00 ± 1.48	11.00 ± 0.74	**0.001**
Gaxiu	TB (g/m^2)	74.70 ± 13.07	69.65 ± 12.56	0.529
	GB (g/m^2)	21.07 ± 3.69	31.68 ± 5.59	**0.021**
	FB (g/m^2)	55.06 ± 11.79	43.52 ± 15.91	**0.021**
	Plant species richness	15.50 ± 2.22	19.00 ± 2.97	**0.006**

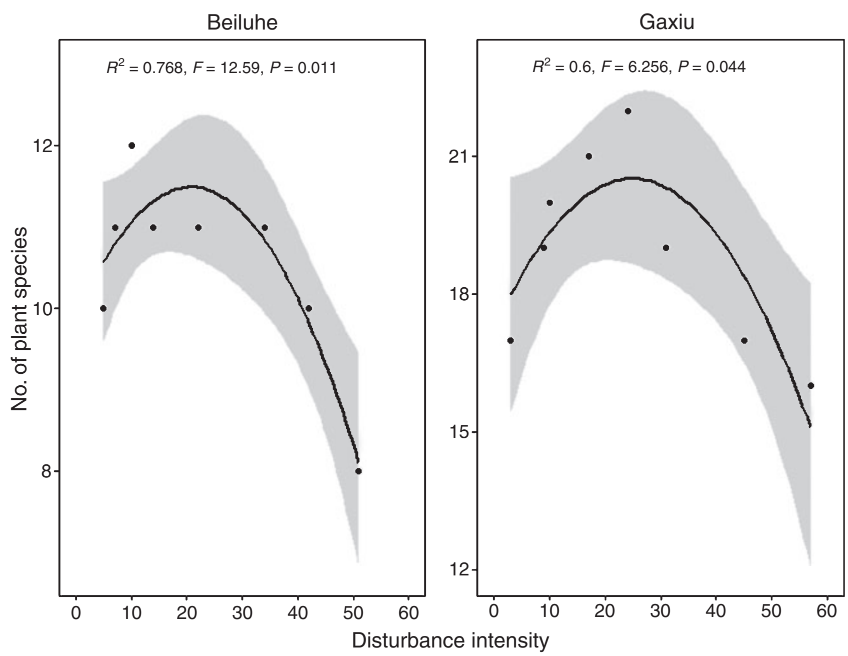

Fig. 5. The number of species (median ± median absolute deviation) in disturbed areas under different disturbance intensities at Beiluhe Basin ($Y = -0.004X^2 + 0.154X + 9.890$. Y, No. of plant species. X, disturbance intensity) and Gaxiu Basin ($Y = -0.005X^2 + 0.262X + 17.250$. Y, No. of plant species. X, disturbance intensity) based on linear model. For detailed visualisation of the relationship between disturbance intensity and the number of plant species, an adjusted local smoothed regression line (black) with its 95% confident interval (grey) was used. Disturbance intensity, active burrow entrances per plot.

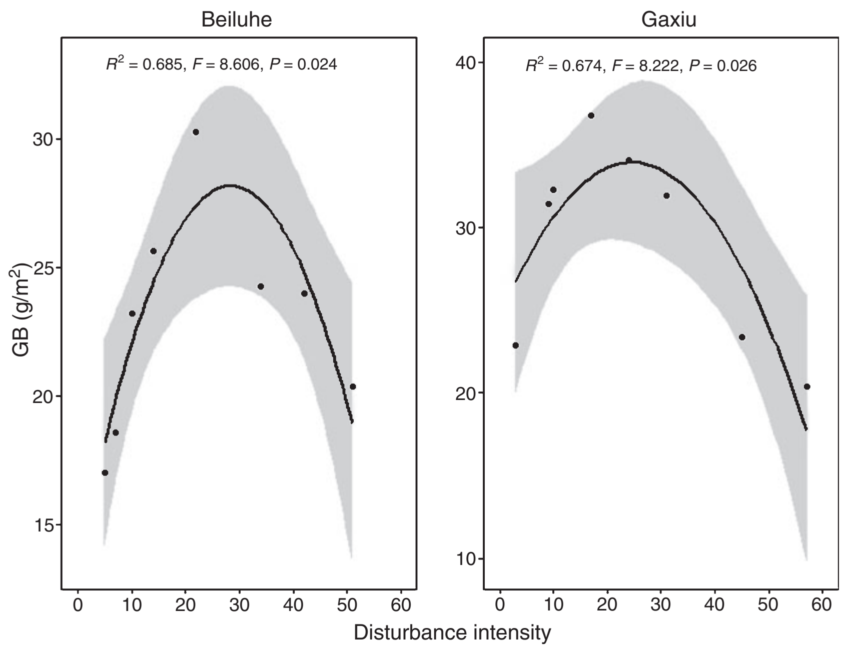

Fig. 6. The biomass of graminoid plant (median ± median absolute deviation) in disturbed areas under different disturbance intensity from Beiluhe Basin ($Y = -0.018X^2 + 1.032X + 13.531$. Y, GB. X, disturbance intensity) and Gaxiu Basin ($Y = -0.015X^2 + 0.760X + 24.587$. Y, GB. X, disturbance intensity) based on linear model. For detailed visualisation of the relationship between disturbance intensity and GB, an adjusted local smoothed regression line (black) with its 95% confident interval (grey) was used. Disturbance intensity, active burrow entrances per plot. GB, graminoid biomass.

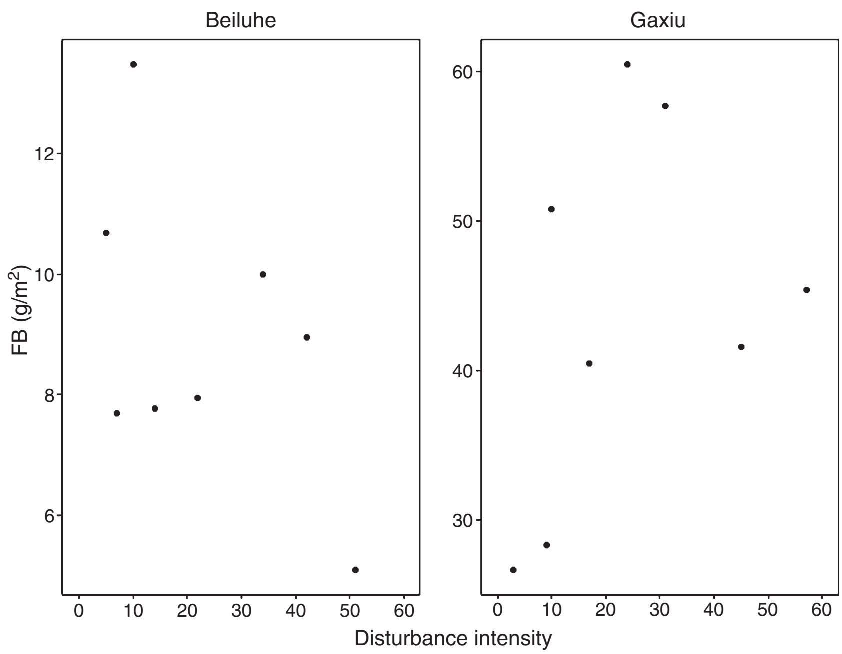

Fig. 7. The biomass of forb plant (median ± median absolute deviation) in disturbed areas under different disturbance intensities at Beiluhe Basin and Gaxiu Basin based on linear model. Disturbance intensity, active burrow entrances per plot. FB, forb biomass.

Table 3. Effects of plateau pika disturbances on the relationship of plant biomass and soil nutrients
SM, STN are defined as Table 1. TB, GB, FB are defined as Table 2

Survey sites				*R*-square	Adjusted r^2	*P*	Relationship
Beiluhe	Undisturbed (*n* = 40)	TB	STN	0.590	0.568	0.000	+
			SM			0.001	+
		GB	STN	0.599	0.578	0.000	+
			SM			0.000	+
		FB	STN	0.535	0.510	0.000	+
			SM			0.002	+
	Disturbed (*n* = 40)	TB	STN	0.893	0.885	0.001	+
			SM			0.000	+
			STP			0.000	+
		GB	STN	0.825	0.816	0.000	+
			STP			0.000	+
		FB	SM	0.728	0.713	0.000	+
			STP			0.009	+
Gaxiu	Undisturbed (*n* = 40)	TB	STN	0.510	0.483	0.001	+
			SM			0.000	+
		GB	STN	0.278	0.259	0.000	+
		FB	STN	0.322	0.286	0.003	+
			SM			0.021	+
	Disturbed (*n* = 40)	TB	STN	0.510	0.483	0.001	+
			SM			0.000	+
		GB	STN	0.915	0.913	0.000	+
		FB	SM	0.400	0.384	0.001	+

significantly different among disturbance intensities at two sites (Fig. 7).

Effects of plateau pika disturbances on the relationship of plant biomass and soil nutrients and moisture

Stepwise multiple regression showed that plateau pika disturbances altered the contribution of soil moisture and nutrients to plant productivity because the predominant soil factors for TB, GB and FB were not completely the same between disturbed areas and undisturbed areas at two sites (Table 3), indicating that plateau pika disturbances altered the correlation relationship between soil moisture and nutrients and plant productivity.

At Beiluhe Basin in the Qinghai province, SM and STN were predominant factors for TB in undisturbed areas, whereas SM and STN together with STP were predominant factors in disturbed areas; GB was predominantly regulated by STN and SM in undisturbed areas, whereas it was predominantly regulated by STN and STP in disturbed areas; the predominant soil factors for FB were SM and STN in undisturbed areas, whereas it became SM and STP in disturbed areas.

At Gaxiu Basin in the Gansu province, the predominant soil factors were SM and STN for TB and it was STN for GB in undisturbed and disturbed areas. However, the predominant soil factors for FB were SM and STN in undisturbed areas, whereas it was SM in disturbed areas.

Discussion

Effects of plateau pika disturbances on soil nutrients and moisture

Our study demonstrated that plateau pika disturbances increase SOC and STN contents on vegetated land of the same alpine meadow type, which are similar to some results found on bare land in previous experiments, in which rodent disturbances increase STN content (Hagenah and Bennett 2013), soil total carbon (Yurkewycz *et al*. 2014), soil nitrogen and organic matter (Wei *et al*. 2006; Liu *et al*. 2010). Plateau pika disturbances decrease SM content on vegetated land of the same alpine meadow type, as is also reported in meadow steppe at the Three Rivers Headwaters Region of the Qinghai-Tibet Plateau (Liu *et al*. 2013*b*). In vegetated land, rodent activities (foraging, burrowing, excretion, burial, storage, producing bare patches) do not only bury the vegetation but also mix soil up with decomposed uneaten food caches and deposited urine or faeces (Huntly and Inouye 1988), which increase the input of organic matter and encourage the disturbed areas to become relatively nutrient-rich (Canals *et al*. 2003; Yurkewycz *et al*. 2014), resulting in an increase of SOC and STN. These imply that rodent disturbances do not only increase SOC and STN in bare land (Wei *et al*. 2006; Liu *et al*. 2010; Hagenah and Bennett 2013; Yurkewycz *et al*. 2014), but also increase SOC and STN in vegetated land.

This study shows that both STP and STK contents in vegetated land are not different between disturbed areas and undisturbed areas, and this is not similar to the results from tuco-tuco disturbances on mound soils, in which rodent activities redistribute the soil parent materials of mounds in southern Brazil (Galiano *et al*. 2014). However, plateau pika activities in this study have not redistributed soil parent materials in vegetated land, resulting in no difference in soil phosphorus and potassium between disturbed areas and undisturbed areas.

Our results present an interesting phenomenon that SOC and STN content in disturbed areas is closely related to disturbance intensity of plateau pika, indicating that SOC and STN contents are higher at intermediate disturbance intensities than those at lower or higher disturbance intensities, and this is possibly related to decomposition rate and input of organic matter (Cai *et al*. 2016; Wang *et al*. 2016). When compared with low disturbance intensities, intermediate disturbance intensities bury more plant materials, decomposed uneaten food caches and deposited urine or faeces, resulting in an increase of SOC and STN. Compared with intermediate disturbance intensities, higher disturbance intensities stimulate soil microbial activity by largely increasing soil temperature and aeration, and decreasing soil moisture (Desmet and Cowling 1999; Liu *et al*. 2013*b*), which encourages the organic matter to decompose more rapidly and accelerates the rate of mineralisation (Guo *et al*. 2012*b*), resulting in a decrease of SOC and STN contents. These findings demonstrate that the influence of rodent disturbances on soil nutrients on vegetated land is not only dependent on whether or not the rodent is present, but also is dependent on its disturbance intensities.

Effects of plateau pika disturbances on plant richness diversity and productivity

Plateau pika disturbances increase the number of plant species, as well as other rodents do, such as plains pocket gopher (Rogers *et al*. 2001), kangaroo rat and mole rat (Davidson *et al*. 2008), and prairie dog (Hagenah and Bennett 2013). Why does plateau pika disturbance increase the number of plant species? First, plateau pika activities are likely to enhance the environmental heterogeneity, which opens up gaps for opportunistic plant species (Hagenah and Bennett 2013); second, plateau pika disperses the plant seeds into bare patches via its carry behaviour and its faeces; finally, the burrow of plateau pika is the only habitat home for the snow finch (*Montifringilla ruficollis*) (Liu et al. 2013*a*), and this bird also disperses the plant seed into bare patches and other regions. Seed plants, such as *Melissilus ruthenicus* and *Artemisia frigida* in the Beiluhe Basin and *Oxytropis ochrocephala*, *Astragalus nivalis*, and *Euphrasia pectinata* in the Gaxiu Basin, settle down in bare patches, contributing to the increase the number of plant species.

The number of plant species first increase and then decrease in disturbed areas as the plateau pika disturbance intensity increases in two sites and this is also previously reported in disturbances of Stoliczka's voles and plateau pika on arid rangeland in the high altitude Trans-Himalaya (Bagchi *et al*. 2006), which supports the intermediate disturbance theory, as well as effects of grazing disturbance on plant species richness (Aryal *et al*. 2015). At the higher disturbance intensities, the habitat of alpine meadow become dry due to reduction of soil moisture (Liu *et al*. 2013*b*), and some hygrophytes disappear from plant communities (Pang *et al*. 2015), which contributes to the decrease in number of plant species.

Plateau pika disturbances have no significant impacts on TB of alpine meadow, and this is similar to the results from plains pocket gopher disturbance (Adams *et al*. 2010), but differs from mole rat disturbances (Hagenah and Bennett 2013). Surprisingly, this is also different from the effect of plateau pika disturbances on meadow steppe (Liu *et al*. 2013*b*). These findings demonstrate that the influence of rodent disturbances on TB not only varies with different regions but also with grassland type even if in the same region. However, plateau pika disturbances increase GB while decreasing FB. On the one hand, plateau pika disturbances increase STN content, which encourages the nitrogen-loving graminoid plants to grow well (Pecháčková and Krahulec 1995); on the other hand, plateau pika prefers forbs to graminoids (Zhao *et al*. 2013), which alleviates the competition pressure of graminoids. The increase in GB and no change in TB contribute to the reduction of the FB in disturbed areas. In this study, GB shows a unimodal trend as the plateau pika disturbance intensity increases, which responds to the variation of STN content. This implies that foraging by rodents not only results in increasing grazing quality of grassland (Davidson *et al*. 2012), but also that the optimal rodent disturbance intensities are more important to enhance the grazing quality of the alpine meadow.

Effects of plateau pika disturbances on soil–plant interactions

Plant–soil interaction can play a major role in the capacity of alpine meadow ecosystems to adapt to rodent disturbance. This study finds that STN and SM are predominant factors for plant productivity rather than SOC and STK in disturbed areas and undisturbed areas at both sites, and plateau pika disturbances make STP a predominant factor at Beiluhe Basin rather than Gaxiu Basin. At Beiluhe Basin, low STP content and its weak availability due to low soil moisture (Dijkstra *et al*. 2015) in disturbed areas leads STP to become the predominant factor for plant productivity. Although relatively low soil moisture caused by plateau pika disturbance reduces the soil phosphorus availability at the Gaxiu Basin, higher STP content is still able to meet the requirements of plant growth. Consequently, STP is still not the predominant factor for plant productivity in disturbed areas at Gaxiu Basin. As far as SM is concerned, it is one of the predominant factors for GB in undisturbed areas at Beiluhe Basin with relatively high soil moisture, and is not the predominant factor at Gaxiu Basin with relatively low soil moisture because graminoid plants grow better in relatively dry environments than in wet environment (Bowman *et al*. 1993, 1995). Plateau pika disturbances reduce SM, which create the suitable conditions for graminoid plant growth, and thus means that SM cannot be a predominant factor for GB in disturbed areas. Conversely, relatively low soil moisture in disturbed areas is the predominant soil factor for FB because forb plants do not grow well in dry environments (Bowman *et al*. 1993, 1995). STN is the predominant factor for GB and FB in undisturbed areas due to its low content and it is still the predominant factor for GB and is not the predominant factor for FB in disturbed areas because high STN is necessary for nitrogen-loving graminoid plants to grow well. Plateau pika disturbances alter the predominant soil factors for plant biomasses (TB, GB, FB), and the predominant factors, which are STN, SM or their combination in undisturbed areas become STN, SM and STP and their different combination in disturbed areas, indicating that plateau pika disturbances change the predominant soil factors for plant biomass.

Conclusion

Our findings show that plateau pika disturbances increase SOC, STN, GB and the number of plant species, and decrease SM and FB, although they have no significant impacts on STP, STK and TB on vegetated land in the same alpine meadow type. Plateau pika disturbances alter the contribution of soil moisture and nutrients to plant biomass. This study also has verified that the optimal disturbance intensities of plateau pika are beneficial to the grazing quality of alpine meadow. Therefore, the core of plateau pika management is to find the optimal disturbance intensities rather than eradication in the Qinghai-Tibetan plateau, China, and this will help us better understand the role of plateau pika in alpine meadow ecosystems.

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Appendix 1. Plant species in undisturbed areas and disturbed areas of each site

Beiluhe		Gaxiu	
Undisturbed	Disturbed	Undisturbed	Disturbed
Androsace tapete	*A. tapete*	*Ajuga ovalifolia*	*A. ovalifolia*
Aster flaccdius	*A. flaccdius*	*Anemone obtusiloba*	*A. obtusiloba*
–	*Artemisia frigida*	*Anemone obtusiloba*	*A. obtusiloba*
Astragalus polycladus	*A. polycladus*	*Anemone rivularis* var. *flore-minore*	*A. rivularis* var. *flore-minore*
Carex atrofusca	*C. atrofusca*	*Anemone trullifolia*	*A. trullifolia*
Carex moorcroftii	*C. moorcroftii*	–	*Astragalus nivalis*
Festuca rubra	*F. rubra*	*C. moorcroftii*	*C. moorcroftii*
Kobresia pygmaea	*K. pygmaea*	*Cremanthodium lineare*	*C. lineare*
Kobresia tibetica	*K. tibetica*	*Elsholtzia densa*	*E. densa*
Lancea tibetica	*L. tibetica*	*Elymus nutans*	*E. nutans*
Leontopodinm nanum	*L. nanum*	*Euphorbia esula*	*E. esula*
Oxytropis ochrocephala	–	–	*Euphrasia pectinata*
Poa poophagorum	*P. poophagorum*	*Gentiana dahurica*	*G. dahurica*
–	*Melissilus ruthenicus*	*Gentiana sinoornata*	*G. sinoornata*
–	*Oxytropis ochrocephala*	*Geranium pylzowianum*	*G. pylzowianum*
–	*Sanguisorba arenaria*	*K. pygmaea*	*K. pygmaea*
–	–	*Lamiophlomis rotata*	*L. rotata*
–	–	*L. nanum*	*L. nanum*
–	–	–	*Lespedeza davurica*
–	–	*Locea tibetica* Hook.f.er Thoms	*L. tibetica* Hook.f.er Thoms
–	–		*O.ochrocephala*
–	–	*Pedicularis tricolor*	*P. tricolor*
–	–	–	*Plantago asiatica*
–	–	*Pleurospermum camtschaticum*	–
–	–	*Polygonum viviparum*	*P. viviparum*
–	–	*Potentilla anserina*	*P. anserina*
–	–	*Potentilla fragarioides*	*P. fragarioides*
–	–	*Rheum palmatum*	*R. palmatum*
–	–	*Saussurea macrota*	*S. macrota*
–	–	*Swertia bimaculata*	*S. bimaculata*
–	–	*Thalictrum alpinum* var. *elatum*	*T. alpinum* var. *elatum*
–	–	*Tibetia himalaica*	*T. himalaica*