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Soil nutrient changes induced by the presence and intensity of plateau pika (*Ochotona curzoniae*) disturbances in the Qinghai-Tibet Plateau, China

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ABSTRACT

The plateau pika (*Ochotona curzoniae*), one of the main bioturbators, creates extensive disturbances in the soil of the alpine meadow of the Qinghai-Tibet Plateau (QTP). This study investigated the effects of the presence and intensity of plateau pika disturbances on the main soil nutrients of the *Kobresia pygmaea* meadow across three study sites in the QTP by using the method of counting the active burrow entrance densities of plateau pika in the field as a representation of the disturbance intensity. Our results showed that the presence of plateau pika significantly increased the soil total nitrogen (TN), soil organic carbon (SOC) and total phosphorus (TP) concentrations and decreased the available phosphorus (AP) concentrations across the three study sites. The presence of plateau pika increased the NO_3^--N and NH_4^+-N concentrations in Luqu County and Maqu County, but had no significant effect on these concentrations in Gonghe County. The soil TN, SOC and TP concentrations showed a downward parabola and the NO_3^--N, NH_4^+-N and AP concentrations showed an upward parabola as the intensity of the disturbances increased in Luqu County and Maqu County. These soil nutrients had a threshold (inflection point) of 475 (475 ± 90) burrow entrances per ha. However, the soil TN, SOC and TP concentrations increased linearly while the NO_3^--N, NH_4^+-N and AP concentrations decreased linearly with the increasing intensity of disturbances in Gonghe County (≤512 burrow entrances per ha). These results implied that the soil nutrient changes induced by plateau pika disturbances are not only related to their presence but are also related to the intensity of the disturbances, and that the most appropriate disturbance intensity (475 (475 ± 90) burrow entrances per ha) of plateau pika was beneficial to the storage of soil carbon and nitrogen in the alpine meadow in the QTP.

1. Introduction

Soil, an essential part of grasslands, physically supports primary producers and decomposers and maintains biotic communities in grassland ecosystems (Brady and Weil, 1996; Lavelle et al., 1997; Dominati et al., 2010; Eisenhauer et al., 2011; Bueno et al., 2013) by regulating nutrient cycling or material-energy flows (Brady and Well, 1996; Lavelle et al., 1997). However, the soil properties of grassland ecosystems are usually disturbed by various direct and indirect soil bioturbators (Jones et al., 1997; Gabet et al., 2003; Richards, 2009; Resner et al., 2015). These bioturbators often alter the soil nutrients concentration of grassland by redistributing soil nutrients within soil profiles (Villarreal et al., 2008), which occurs rapidly on the temporal and spatial scales when compared to other plant-driven and geologic processes (Fleming et al., 2014). Wild boar rooting increases the soil total nitrogen and NO_3^--N concentrations while it decreases the NH_4^+-N concentrations in the alpine grassland of the Spanish Central Pyrenees (Bueno et al., 2013). The burrowing and casting activities of earthworms (*Allolobophora hrabei*) induce an increase in the concentrations of soil dissolved organic carbon and archaea richness, which enriches the available nutrients in the steppe grasslands of southern Moravia in the Czech Republic (Jirout and Pižl, 2014). Tuco-tucos (*Ctenomys Mendocinus*) disturbances soften the topsoil and increase soil nitrogen, phosphorus and potassium while decreasing soil calcium in the South Brazilian coastal plain (Malizia et al., 2000; Galiano et al., 2014). These effective studies show that soil bioturbators alter the spatial and temporal heterogeneity of soil nutrients and become important agents for maintaining species diversity and soil nutrient cycling in grassland ecosystems.

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The plateau pika (*Ochotona curzoniae*), an important bioturbator, is an endemic and dominant small animal of the alpine meadow ecosystem in the Qinghai-Tibet Plateau (QTP) (Smith and Foggin, 1999; Lai and Smith, 2003). For a long time it has been considered to be the main cause of the alpine meadow degradation in China by its foraging and digging behavior (Smith and Foggin, 1999; Guo et al., 2012; Liu et al., 2013). Plateau pikas alter the soil properties of the alpine meadow through its roles as a forager of vegetation, constructor of extensive burrow networks and producer of bare patches (Smith and Foggin, 1999; Sun et al., 2015a; Wu et al., 2015). For example, the burrowing behavior of plateau pikas usually creates a complex mosaic of disturbed patches of different sizes (Davidson and Lightfoot, 2008; Wu et al., 2015), redistributing soil among different horizons, and these alter the concentration and distribution of the soil nutrients and further affect the ecological functions of the alpine meadow (Zhou et al., 2010; Fleming et al., 2014; Qin et al., 2015). Published findings illustrate that the effectiveness of plateau pika disturbances on soil properties is dependent not only on the presence but also on the intensity of the disturbances (Zhou et al., 2010) because severe soil erosion and degradation often occur with the high intensity of plateau pika disturbance rather than low intensity (Wangdwei et al., 2013). Soil nutrients are remarkably sensitive in the alpine meadow due to cool temperatures and a relatively short growing season in the QTP (Körner, 2003; García-González, 2008), and the sensitivity of soil nutrients may be exacerbated by plateau pika disturbances. Studies indicate that the presence of plateau pika accelerates soil erosion and vegetation degradation, reduces the palatable forage proportion for domestic livestock (Wei et al., 2007; Dong et al., 2013), and increases CO_2 emitted into the atmosphere (Qin et al., 2015). Some other studies argue that the presence of plateau pika stimulates microbial activity, improves organic matter decomposition and soil nitrogen availability (Villarreal et al., 2008; Zhang et al., 2016) and increases soil organic matter in the topsoil layer (Li et al., 2006). Meanwhile, the presence of plateau pika often creates microhabitats in the alpine meadow, resulting in an increase in plant species richness and "hot spots" of biological activity over longer timescales (Smith and Foggin, 1999; Davidson and Lightfoot, 2008; Zhang et al., 2016). These results indicate that the responses of the soil properties to the presence of plateau pika are not consistent in a partial microenvironment. The population size of plateau pika is a direct indicator that can be used to evaluate whether these impacts are beneficial or detrimental to alpine meadow ecosystems (Guo et al., 2012; Sun et al., 2015b).

There are also several ongoing debates concerning the effects of the intensity of plateau pika disturbances on the soil nutrients of the alpine meadow. Sun et al. (2015b) and Liu et al. (2013) reported that soil organic carbon, total nitrogen, total phosphorus and NH_4^+-N decrease but that soil temperature and NO_3^--N increase with the increased intensity of plateau pika disturbances. Guo et al. (2012) indicated that moderate disturbances by plateau pika increase the soil organic matter, total nitrogen and total phosphorus contents. However, Peng et al. (2015) argued that soil organic carbon, total nitrogen and inorganic nitrogen (NO_3^--N and NH_4^+-N) had no obvious trend with the increasing intensity of plateau pika disturbances. These findings provide useful information for understanding the role of plateau pika in the alpine meadow ecosystem, but these studies ignored the changes of dominant plant species in regard to different disturbance intensity areas across different grassland types. This creates a dilemma of whether the changes in the soil nutrients result from the intensity of plateau pikas disturbances or from the difference in the grassland types. Therefore, it is necessary to indentify the changes in the soil nutrients in same alpine meadow type, which will clarify the actual response of the soil nutrients to the intensity of plateau pika disturbances.

The *Kobresia pygmaea* meadow is the main alpine meadow type and its area is larger than areas of other alpine meadow types in the QTP. Its dominant plant is *K. pygmaea*, with low height and high nutritional value (Li et al., 2013), belonging to the *Cyperaceae*. Thus, the *K. pygmaea* meadow not only plays an irreplaceable role in sustaining native livestock production and biodiversity, conserving water and preventing soil erosion in the QTP (Wang et al., 2008; Wu et al., 2015), but it is also a good habitat with very easy access for plateau pikas due to its relatively low height of vegetation, which provides an open window for plateau pikas to detect and avoid predators (Wangdwei et al., 2013). Thus, the *K. pygmaea* meadow is a representative example of how the plateau pika dramatically affects soil properties. This study aimed to assess whether the presence and intensity of plateau pika disturbances affected the soil nutrients across three study sites where they share the common *K. pygmaea* meadow. Specifically, we hypothesized that: (1) the response of soil nutrients to the presence and intensity of plateau pika disturbances is inconsistent; (2) different intensities of plateau pika disturbances have different influences on the soil nutrients; (3) the response of the three study sites to the presence and intensity disturbances of plateau pika is consistent; (4) an appropriate intensity of plateau pika disturbance is beneficial to soil nutrients in the QTP. This study will be beneficial for understanding the influence of the presence of the plateau pika and its disturbance intensity on soil properties.

2. Materials and methods

2.1. Study area description

The study area was located in Luqu County (102°18′37″ E, 34°20′36″ N), Maqu County (101°53′15″ E, 33°40′41″ N) and Gonghe County (99°35′46″ E, 36°44′34″ N) in the QTP of China. The altitudes of the three study sites are 3550 m, 3530 m and 3750 m above sea level, respectively. The climate of the three study sites is the typical plateau continental climate that is windy, cold, and humid. The average annual temperature is 1–3 °C, with a minimum mean monthly temperature that falls below −10 °C in January and a maximum mean that rises above 12 °C in July. The mean annual precipitation is 60–80 cm in Luqu County and Maqu County and 25–50 cm in Gonghe County, 80% of which falls in the short summer growing season during the period of June–September. The mean annual potential evaporation is 110–130 cm in Luqu County and Maqu County and 80–100 cm in Gonghe County. The alpine meadow is widely distributed in the study area and is the major type of natural grassland in the QTP, which plays an irreplaceable role in water conservation as well as in maintaining the food safety, air quality, and ecological barrier of the Yellow River Basin (Qi et al., 2008; Feng et al., 2010).

The *K. pygmaea* meadow is the main alpine meadow type in the three study sites where plateau pikas are present. For the purposes of this study, our sampling was restricted to *K. pygmaea* meadow at the three study sites. The dominant plant of *K. pygmaea* is perennial forbs and endemic species, and its height is approximately 1–3 cm. The main associated plant species are *Elymus nutans* and *Poa pratensis* of the *Poaceae*, *Anemone obtusiloba* and *A. rivularis* of the *Ranunculaceae*, *Potentilla anserine* and *P. fragarioides* of the *Rosaceae*, and *Saussurea hieracioides* of the *Asteraceae*. The soil type is subalpine meadow soil, according to the Chinese soil classification system (Gong, 2001). The soil is characterized by the presence of a mattic epipedon at approximately 7 cm in the topsoil, which is an organic matter-rich soil horizon. This alpine meadow sustains yaks and Tibetan sheep production via warm and cold season pasture rotational grazing.

2.2. Experimental design

The experiment was designed to analyze the presence/absence (disturbed/undisturbed) of plateau pikas and intensity comparisons within the presence treatments. The field surveys at the three study sites were carried out in the winter-grazed *K. pygmaea* alpine meadow (i.e., no grazing in growth season) during August 2015. The disturbed areas, with the presence of plateau pika, were identified by the presence of a heterogeneous mosaic of bare patches, which are easily visible and differ from the signs of disturbances caused by other mammal species. Undisturbed areas, with the absence of plateau pikas and bare patches, were completely covered with the *K. pygmaea* meadow. The undisturbed areas were established adjacent to the disturbed areas to guarantee the disturbed areas and undisturbed areas shared the same dominant plants and similar vegetation composition. The distance between the disturbed areas and undisturbed areas was over 1 km to form a buffer zone (Peng et al., 2015; Sun et al., 2015b). There were no obvious topographical differences between paired survey locations of the disturbed areas and undisturbed areas. Thus, these were paired disturbed/undisturbed areas within each study site, and the “disturbed” and “undisturbed” areas were regarded as two independent samples for each study site. Because the plateau pika is a social animal that moves and produces 2–5 litters (litter size range = 2–7) at 3-week intervals between each litter in the breeding season of April to August, it was difficult to estimate the plateau pika population directly. Active burrows, as their dwellings, are their main activity assembly areas and disturbance areas. Based on the methods from previous studies (Johnson and Collinge, 2004; Guo et al., 2012; Sun et al., 2015a), we used “active burrow entrance densities” to reflect plateau pika population changes and disturbance intensities. The “plugging tunnels method” is a way to identify active burrow entrance and count them in disturbed areas (Guo et al., 2012; Sun et al., 2015a; Wu et al., 2015).

At each study site, 20 plots, measuring 25 m × 25 m, were selected, and 10 plots were distributed within and 10 were outside the areas disturbed by plateau pika. In the disturbed areas, we investigated the active burrow entrance densities for each plot by the “plugging tunnels method,” which took at least 4 days to complete (Guo et al., 2012; Sun et al., 2015a; Wu et al., 2015), and these surveys were conducted in a relatively fixed time sequence at each plot between 09:00 and 11:30 in relation to the high frequency activities of plateau pika (Zeng and Lu, 2009).

We used a random sampling design to collect soil samples from the disturbed areas and undisturbed areas, and five subplots with a size of 1 m × 1 m were randomly selected in each plot. The dominant species of these five subplots were same and vegetation cover and height were similar, which confirms consistency between sites and disturbed/undisturbed areas. In each subplot, the soil-drilling method was used to collect three soil samples randomly within each subplot, and plant litter from the soil surface was sieved out prior to sampling. Three soil samples from the same subplot were disaggregated and thoroughly mixed to provide a homogeneous and composite sample that was representative of the subplot (n = 1 soil samples/subplot, 300 soil samples in total). A cylindrical metal core sampler with a 5 cm diameter was used to extract a soil sample from a depth of 20 cm because most plant biomass is within the top 10 cm of soil (Bueno et al., 2013) and, generally, the plateau pika burrows do not go deeper than 20 cm (Wei et al., 2006). The composite soil samples were stored in a sealed sampling bag and transported on ice before being placed in a laboratory freezer below 4 °C. The geographical coordinates of each sampling locations were recorded using a handheld GPS (Garmin eTrex 201X, Garmin, USA).

2.3. Soil analyses

Each composite soil sample was air-dried at room temperature and pulverized. The dried soil samples were sieved through a 2-mm wire mesh to remove large particles (stones and gravel), loose vegetative debris and visible roots as much as possible and were used to analyze the soil nutrient concentrations. Total nitrogen (TN) was measured via the Kjeldahl procedure (Foss Kjeltec 8400, FOSS, DK) (Nelson and Sommers, 1982). Soil organic carbon (SOC) was determined using the Walkley–Black method (Nelson and Sommers, 1982). Total phosphorus (TP) was measured by Mo-Sb colorimetry (UV-2102C, UNICO, Shanghai, China), and total potassium (TK) was determined by flame photometry (Model 2655-00 Digital Flame Analyzer, Cole-Parmer Instrument Company, Chicago, IL, USA) after the soil was digested with perchloric and nitric acid (Nelson and Sommers, 1982). Available nitrogen (nitrate nitrogen and ammonium nitrogen) was extracted with potassium chloride (KCl, 2 mol L^{-1}), and the concentrations were measured by the flow injection method (FIAstar 5000 Analyzer, FOSS, DK). Available potassium (AK) was extracted by NH_4OAc and was then measured by flame photometry (Nelson and Sommers, 1982). Available phosphorus (AP) was extracted by $NaHCO_3$ and then measured by Mo-Sb colorimetry (Nelson and Sommers, 1982).

2.4. Statistical analyses

To determine whether the presence of plateau pika significantly altered the soil nutrients, we used two complementary analyses, a linear mixed model (LMM) and a Wilcoxon-Mann-Whitney test. The LMM was used to analyze the relative effect of the presence of plateau pika on the soil nutrients at the three study sites. Each soil nutrient was the response variable, and the presence/absence of disturbances (Dist.), the three study sites (Site) (that were transformed into dummy variables) and their interactions were introduced as predictors for the LMM. Specifically, the presence/absence of disturbances was added to the model as a random factor, which was assigned to each pair of observations. In addition, the active burrow entrance densities were considered to be the fixed factor, and these were used to construct a regression analysis by a linear model (LM). To select the final regression models, which indicated the effect of the plateau pika disturbance intensity on the soil nutrients, likelihood ratio tests were used to compare the simple linear regression and polynomial regression models.

Wilcoxon-Mann-Whitney tests were used to evaluate the effects of the presence of plateau pika on the soil nutrients in each study site because the soil samples were paired and their normality was not guaranteed (Moore et al., 2008; Bueno et al., 2013). All of the statistical analyses were performed with R Version 3.2.2.

3. Results

3.1. Active burrow entrance densities of three study sites

The field survey results showed that the active burrows entrances of the 10 plots within disturbed areas were 144, 192, 288, 352, 416, 496, 576, 736, 832, and 896 per ha in Luqu County; were 112, 192, 272, 384, 432, 512, 576, 752, 928, and 1040 in Maqu County; and were 32, 80, 112, 128, 176, 208, 240, 416, 464, and 512 in Gonghe County. The active burrow entrances in disturbed areas were significantly different among the three study sites (Fig. 1).

3.2. Effect of the presence of plateau pika on soil nutrients

The presence/absence of disturbances (Dist.) and the three study sites (Site) had significant effects on the soil TN, SOC, TP and AP

Table 1
Soil nutrients in relation to the presence of plateau pika (disturbances) in the three most disturbed sites of the *Kobresia pygmaea* meadow in the Qinghai-Tibet Plateau (QTP) of China, based on Linear Mixed Models.

Response variable	Linear mixed models (Dist. as a random factor)					
	Site		Dist.		Site × Dist.	
	F	p value	F	p value	F	p value
TN (g kg^{-1})	28.117	0.001	23.455	0.001	5.028	0.081
SOC (g kg^{-1})	55.026	0.001	33.336	0.001	3.789	0.150
TP (g kg^{-1})	15.066	0.001	67.025	0.001	9.482	0.009
TK (g kg^{-1})	6.521	0.038	1.499	0.221	0.468	0.791
NO_3^--N (mg kg^{-1})	117.940	0.001	2.121	0.145	25.007	0.001
NH_4^+-N (mg kg^{-1})	72.532	0.001	1.626	0.202	5.153	0.076
AP (mg kg^{-1})	41.109	0.001	42.584	0.001	2.330	0.312
AK (mg kg^{-1})	21.139	0.001	0.289	0.591	0.648	0.723

Each soil nutrient acts as a response variable, while the predictors were as follows: the presence/absence of disturbances (Dist.); the three study sites (Site); and the interaction of both. The factor of Dist., which account for the paired design, acted as a random variable. TN: total nitrogen; SOC: soil organic carbon; TP: total phosphorus; TK: total potassium: AP: available phosphorus; AK: available potassium. Alpha (significance level) = 0.05.

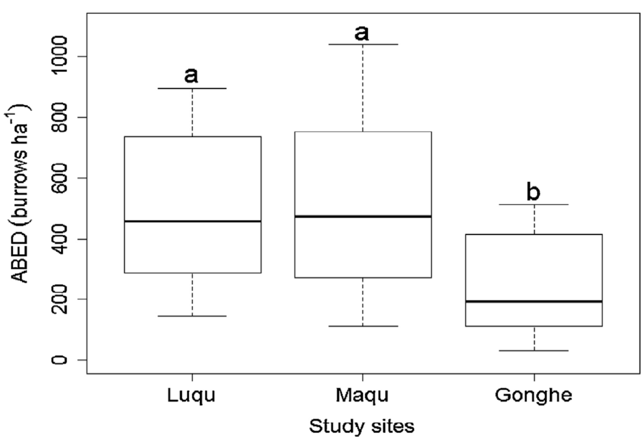

Fig 1. Active burrow entrance densities of plateau pika in the three most extensively disturbed alpine meadows in the Qinghai-Tibet Plateau (QTP) of China. Lower-case letters indicate significant differences among the three study sites based on a non-parametric multiple test at alpha < 0.05. ABED: Active burrow entrance densities.

concentrations, and they had no significant effect on the soil TK and AK concentrations (Table 1). The soil TN, SOC, and TP concentrations in disturbed areas were significantly higher relative to the areas devoid of plateau pika, while the AP concentrations tended to be lower within disturbed areas than in undisturbed areas across all three study sites (Fig. 2).

Regarding the total nutrients in each study site, the soil TN, SOC and TP concentrations in disturbed areas were significantly higher than those in undisturbed areas (Table 2). Among the available nutrients, the AP concentration in disturbed areas was significantly lower relative to the areas devoid of plateau pika. The responses of NO_3^--N and NH_4^+-N concentrations to the presence of plateau pika were site-dependent, they significantly increased in disturbed areas at Luqu County and Maqu County, while were not significantly different between disturbed and undisturbed areas in Gonghe County (Table 2).

3.3. Effects of the plateau pika disturbance intensity on soil nutrients

Most of the soil nutrients in the alpine meadow were strongly influenced by the intensity of the plateau pika disturbances, and the soil TK and AK concentrations showed no significant trends with increasing intensity of plateau pika disturbances (Figs. 3–5). In Maqu County and Luqu County, most of the soil nutrients showed a significant unimodal curvilinearity as the intensity of the plateau pika disturbances increased, with soil TN, SOC and TP showing an obvious opposite trend compared to soil NO_3^--N, NH_4^+-N and AP as the intensity of the plateau pika disturbances increased (Figs. 3 and 4). With the intensification of the activity of the animal, the soil TN, SOC and TP concentrations increased significantly at first and then decreased, peaking at 475(475 ± 90) burrow entrances per ha, whereas the soil NO_3^--N, NH_4^+-N and AP concentrations dropped significantly at first and then rose rapidly and were the lowest at 475(475 ± 90) burrow entrances per ha. However, most of the soil nutrients showed a significant linear relationship with the intensity of plateau pika disturbances in

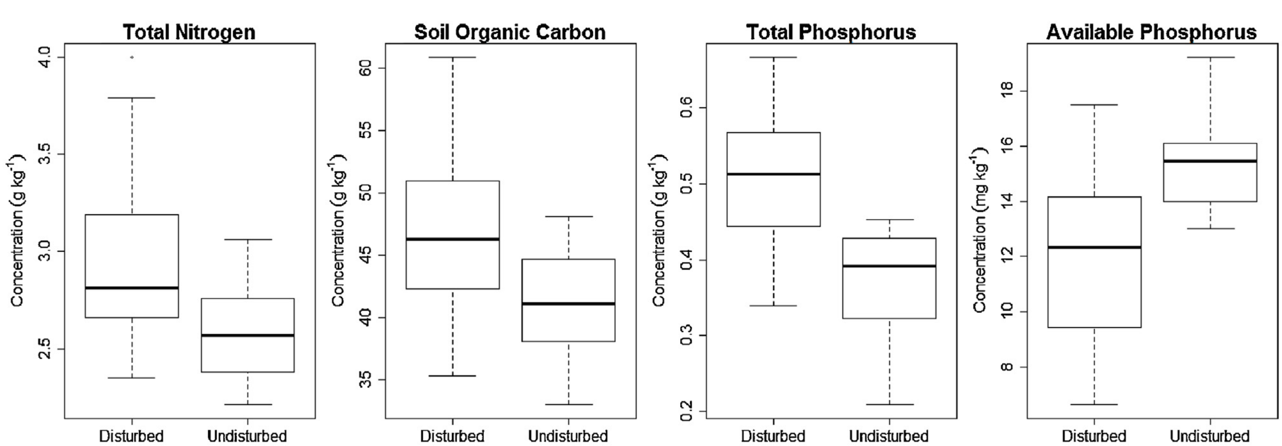

Fig. 2. Values of the significant soil nutrients that differ in undisturbed and disturbed areas according to the active of plateau pika. The values were obtained from the Linear Mixed Models with respect to the presence of plateau pika disturbances in the *Kobresia pygmaea* meadow of Luqu County, Maqu County and Gonghe County (see Table 1).

Table 2
Soil nutrients concentrations (median ± median absolute deviation) in the areas disturbed and undisturbed by plateau pika in Luqu County, Maqu County and Gonghe County in the QTP in China.

Nutrients	Luqu County		p value	Maqu County		p value	Gonghe County		p value
	Undist.	Dist.		Undist.	Dist.		Undist.	Dist.	
TN ($g\,kg^{-1}$)	2.75 ± 0.41	3.14 ± 0.54	0.049	2.44 ± 0.38	2.64 ± 0.22	0.019	2.6 ± 0.45	3.04 ± 0.55	0.001
SOC ($g\,kg^{-1}$)	42.16 ± 6.25	51.43 ± 7.7	0.007	36.28 ± 5.42	40.92 ± 4.86	0.013	44.65 ± 4.1	48.22 ± 4.16	0.023
TP ($g\,kg^{-1}$)	0.29 ± 0.05	0.48 ± 0.13	0.000	0.43 ± 0.07	0.51 ± 0.08	0.007	0.40 ± 0.03	0.52 ± 0.08	0.002
TK ($g\,kg^{-1}$)	22.4 ± 2.57	22.27 ± 3.5	0.199	21.11 ± 2.36	21.5 ± 3.25	0.199	21.56 ± 3.42	21.65 ± 2.94	0.650
NO_3^--N ($mg\,kg^{-1}$)	15.76 ± 2.47	18.47 ± 3.65	0.037	9.32 ± 1.46	10.92 ± 2.16	0.049	14.34 ± 1.77	12.02 ± 2.19	0.584
NH_4^+-N ($mg\,kg^{-1}$)	21.06 ± 2.73	22.54 ± 4.16	0.050	14.8 ± 2.36	16.66 ± 4.31	0.043	16.73 ± 2.2	15.54 ± 2.13	0.290
AP ($mg\,kg^{-1}$)	14.33 ± 2.35	11.03 ± 4.45	0.005	14.52 ± 2.08	11.55 ± 2.44	0.000	16.86 ± 1.38	15.45 ± 2.08	0.049
AK ($mg\,kg^{-1}$)	231.79 ± 34.63	226.48 ± 36.68	0.880	215.91 ± 17.42	211.9 ± 23.8	0.940	234.79 ± 8.19	226.98 ± 11.67	0.199

Significant differences between the disturbed and undisturbed areas were tested by using a Wilcoxon–Mann–Whitney test. TN: total nitrogen; SOC: soil organic carbon; TP: total phosphorus; TK: total potassium: AP: available phosphorus; AK: available potassium; Undist.: Undisturbed areas; Dist.: Disturbed areas. Alpha (significance level) = 0.05.

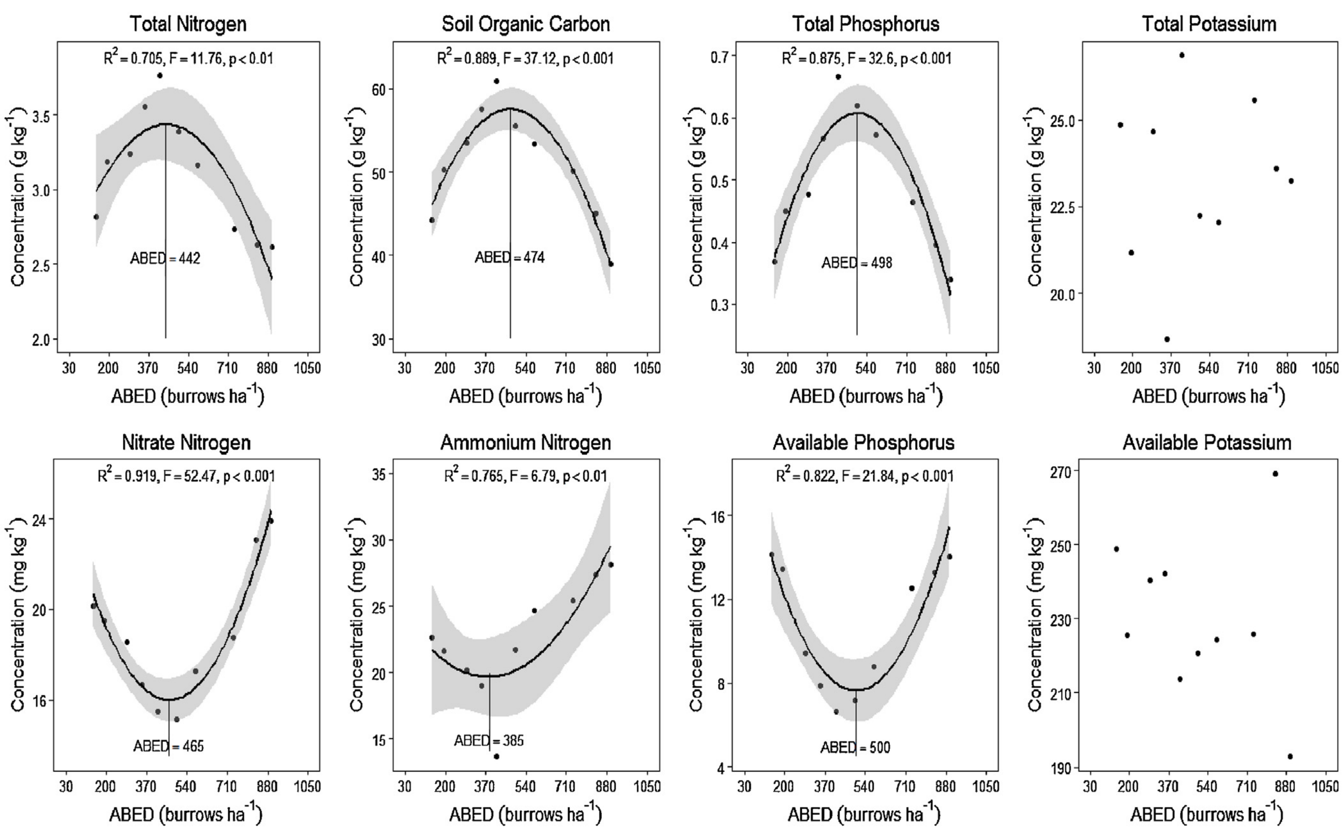

Fig. 3. Soil nutrient concentrations for different intensity disturbances of plateau pika in Luqu County based on a Linear Model. For a detailed visualization of the relationship between the intensity of the disturbances and soil nutrient concentrations, an adjusted local smoothed regression line (black) is shown with its 95% confidence interval in gray. The black vertical lines indicate the level of active burrow entrance densities where the concentration trend of the soil nutrients started to change. ABED: Active burrow entrance densities.

Gonghe County (Fig. 5). The soil TN, SOC and TP concentrations increased linearly, while the NO_3^--N, NH_4^+-N and AP concentrations decreased linearly as the intensity of the plateau pika disturbances increased.

4. Discussion

Plateau pika have co-evolved with the grasslands over millions of years, and they often play key and engineering roles in the *K. pygmaea* meadow ecosystem (Smith and Foggin, 1999; Lai and Smith, 2003). This is the first report on the effect of the presence and intensity of plateau pika disturbances on the soil nutrients in the same alpine meadow type, which presents more information than only the presence or different intensities across different grassland types. Our findings clearly demonstrated a strong link between the presence of plateau pika and the soil nutrients in the *K. pygmaea* meadow, and the presence of plateau pika improves the concentrations of soil TN, SOC and TP. Similar results were also found in the presence of prairie dogs and pocket gophers, both of which have positive effects on soil carbon and nitrogen storage in North America (Yurkewycz et al., 2014; Martínez-Estévez et al., 2013).

There are several reasons that the presence of plateau pika increases the amount of soil TN, SOC and TP rather than TK in disturbed areas. First, the digging and excretion activities of plateau pika improve the surface soil's physical and chemical properties and encourages microorganisms to decompose litter (Dong et al., 2013) because digging burrows softens the topsoil and increases the soil bulk density (lower soil hardness) in disturbed areas (Malizia et al., 2000; Guo et al., 2012), and the excretion activities input organic fertilizer through urine and feces regularly deposited

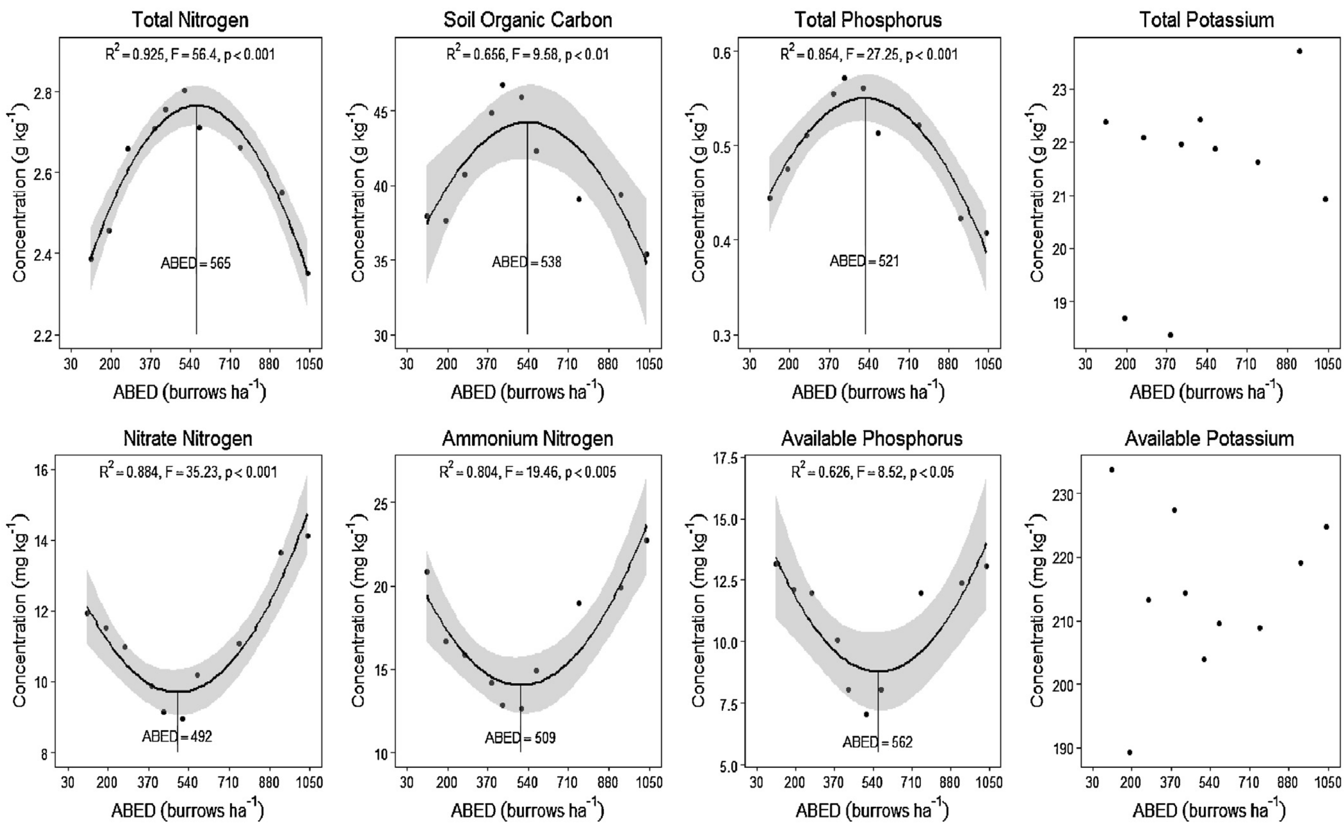

Fig. 4. Soil nutrient concentrations for different intensity disturbances of plateau pika in Maqu County based on a Linear Model. For a detailed visualization of the relationship between the intensity of the disturbances and the soil nutrient concentrations, an adjusted local smoothed regression line (black) is shown with its 95% confidence interval in gray. The black vertical lines indicate the level of active burrow entrance densities where the concentration trend of the soil nutrients started to change. ABED: Active burrow entrance densities.

around disturbed areas (Fleming et al., 2014). Second, the presence of plateau pika increases organic input into soil by burying vegetation in soil (Liu et al., 2013; Galiano et al., 2014; Zhang et al., 2016). Third, plateau pika fragment plants in the process of foraging, which is beneficial to the decomposition of soil litter (Chapman et al., 2003). The above-mentioned actions result in an increase of the soil TN and SOC. Although the soil TP and TK are a conservative soil property and are mainly dependent on the soil's parent material, the presence of plateau pika increases the TP concentration rather than the TK concentration. Soil TP mainly consists of inorganic and organic phosphorus, and the presence of plateau pika increases the organic phosphorus concentration because organic phosphorus increases with the increased accumulation of soil organic material (SOM) (Malizia et al., 2000; Liu et al., 2005). SOM contains soil TK, but its concentration is much lower than that of minerals (Liu et al., 2005). Consequently, the increased input of SOM slightly contributes to the soil TK concentration. Therefore, the presence of plateau pika increases the soil TP concentrations but does not have much effect on the TK concentration under the same soil parent material conditions.

Due to the extremely cool climate in the study area, a large amount of dead roots and litter are stored in the form of organic matter, and this organic matter decomposes slowly (National Soil Survey Office of China, 1998), resulting in a relatively low amount of available nutrients in undisturbed areas of alpine meadow. The presence of plateau pika also significantly increased soil NO_3^--N and NH_4^+-N, decreased soil AP, and had no significant influence on soil AK in Luqu County and Maqu County. The soil NO_3^--N and NH_4^+-N concentrations depend on the mineralization rate of organic matter and microbial activity (Li and Zhang, 2006; Wesche et al., 2007), which are often modified by temperature, soil moisture, and oxygenation (Brady and Weil, 1996; Bueno et al., 2013). The presence of plateau pika breaks up stable aggregates of soil particles (Canals et al., 2003; Zhang et al., 2016) and increases soil moisture and oxygenation by lowering soil hardness in disturbed areas, which enables greater incorporation of litter into soil (Malizia et al., 2000; Guo et al., 2012), resulting in an increase in the nitrogen mineralization rate and a higher available nitrogen concentration of soil in disturbed areas (Curlevski et al., 2014; Sun et al., 2015b). This is supported by the results of other studies, in which pocket gophers (Canals et al., 2003), wild boars (Bueno et al., 2013), plateau zokor (Zhang et al., 2014) and arctic fox (Gharajehdaghipour et al., 2016) increase the soil's available nitrogen concentrations. The soil AP is mainly dependent on the release of soil primary minerals; however, the subalpine meadow soil in the QTP has a phosphorus deficiency (Liu et al., 2005) as well as an available nitrogen deficiency. The presence of plateau pika accelerates the infiltration of top soil moisture into deep soil (Galiano et al., 2014; Zhang et al., 2014), which encourages the AP to deposit into deep soil due to leaching, resulting in a low soil AP concentration in topsoil. Meanwhile, the presence of plateau pika is conducive to plant absorption and the utilization of soil nutrients (Galiano et al., 2014), which may also contribute to the reduction of the soil AP in topsoil. However, the soil NO_3^--N and NH_4^+-N concentrations in disturbed areas tended to be lower than in undisturbed areas, and there were no significant differences between disturbed and undisturbed areas in Gonghe County. This may be attributed to the fact that the intensities of the disturbances in Gonghe County were significantly lower than those in Luqu County and Maqu County. The low intensity of disturbances was less effective on reinforcing the soil mineralization rate than was its ability to promote plant absorption and the utilization of soil nutrients.

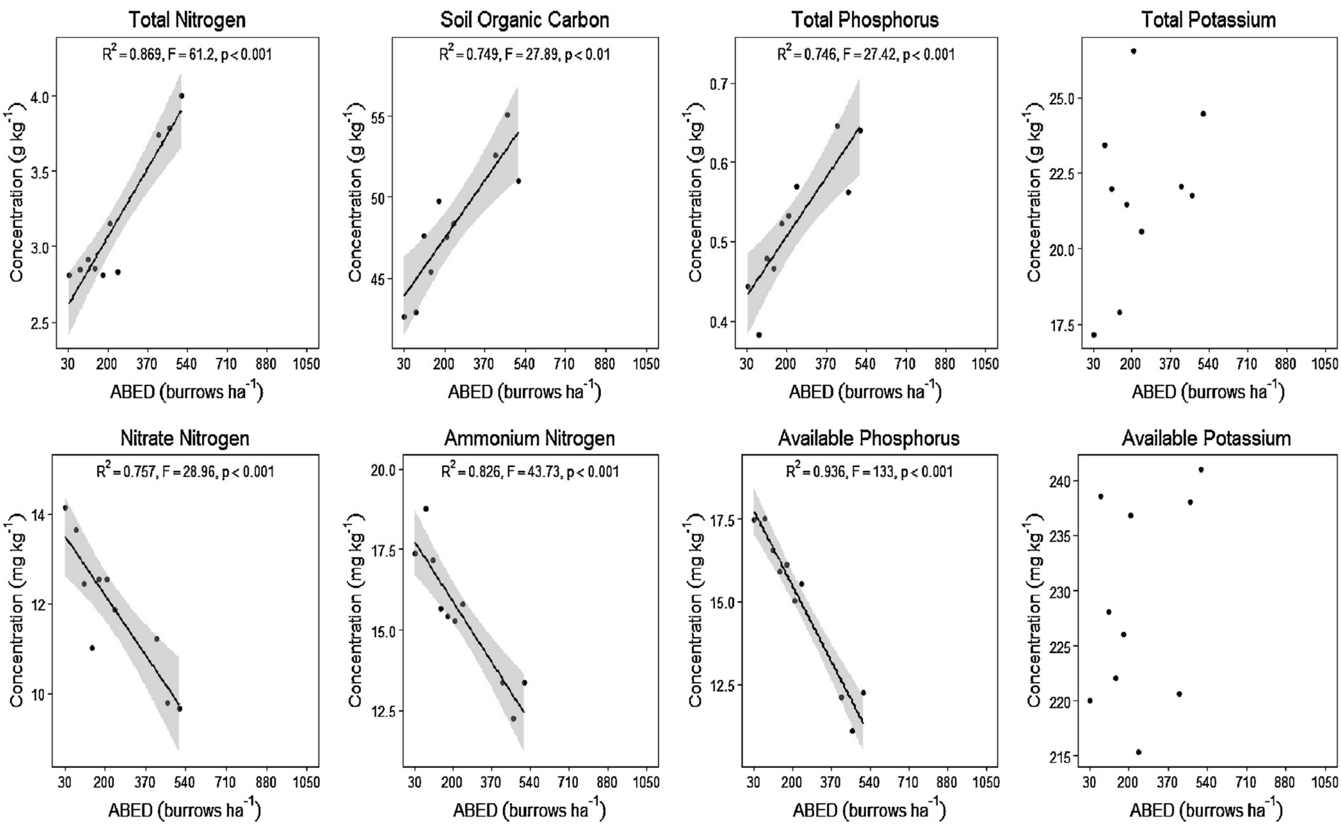

Fig. 5. Soil nutrient concentrations for different intensity disturbances of plateau pika in Gonghe County based on a Linear Model. For a detailed visualization of the relationship between the intensity of the disturbances and the soil nutrient concentrations, an adjusted local smoothed regression line (black) is shown with its 95% confidence interval in gray. ABED: Active burrow entrance densities.

The presence of plateau pika has an effect on the soil nutrients and whether the effect was positive or negative depended on the intensity of the disturbances. Our results show that the soil TN, SOC and TP concentrations had a parabolic shape that extends steadily downward as the intensity of the plateau pika disturbances increased in Luqu County and Maqu County, and the simulation results showed that 475(475 ± 90) burrow entrances per ha was the best disturbance intensity for the TN, SOC and TP concentrations. These results suggest that the positive effectiveness was strongly influenced by the intensity of plateau pika disturbances, implying that the appropriate disturbance intensity, as reflected by the active burrow entrance densities, is conducive to maximizing the storage of soil carbon and nitrogen pools under ideal conditions. However, an excessive intensity of the plateau pika disturbances (active burrow entrance over the threshold of 475(475 ± 90) per ha) was not conductive to the accumulation of SOC, TN and TP, which was also reported in the Guoluo regions in the QTP (Guo et al., 2012). As the intensity of the disturbances increased over the threshold and intensified continuously, there was a decrease in organic matter input, resulting from the low vegetation cover and biomass (Bormann and Sidle, 1990; Liu et al., 2013; Sun et al., 2015b), which caused the soil TN, SOC and TP concentrations to decrease. However, the soil NO_3^--N, NH_4^+-N and AP concentrations dropped significantly at 475(475 ± 90) active burrow entrance densities per ha in Luqu County and Maqu County. This may be ascribed to the fact that a suitable plateau pika presence plays only a small active part in mineralizing soil nutrients and is conducive to plant absorption and the utilization of soil nutrients (Galiano et al., 2014), which might contribute to the reduction of available soil nutrients in topsoil. In Gonghe County, the highest active burrow entrance density was 512 burrow entrances per ha, which is within 475 ± 90 burrow entrances per ha. Therefore, the soil TN, SOC and TP concentrations linearly increased while the NO_3^--N, NH_4^+-N and AP concentrations linearly decreased with the increased intensity of plateau pika disturbances in Gonghe County. High-intensity and frequent disturbances by plateau pika encourage soil oxygen to steadily increase, which strengthens the mineralization speed of organic nitrogen (Brady and Weil, 1996), resulting in increased NO_3^--N and NH_4^+-N concentrations (Wesche et al., 2007; Villarreal et al., 2008).

The responses of the main soil nutrients to the intensity of plateau pika disturbances in this study are different from the results from the Three Rivers Headwaters region (Liu et al., 2013) and Guoluo regions (Guo et al., 2012; Sun et al., 2015b) in the QTP, which ignored the grassland types. Therefore, understanding the response of the main soil nutrients to the plateau pika disturbances should consider not only their presence and intensity but also the grassland type, and these can differentiate the response of the soil properties to plateau pika disturbances (presence and intensity) or to the grassland type.

5. Conclusion

In summary, the presence of plateau pika deeply affects the soil TN, SOC, TP, NO_3^--N, NH_4^+-N and AP rather than the TK and AK in the *K. pygmaea* meadow ecosystem. Specifically, that the presence of plateau pika increases the soil TN, SOC, TP, NO_3^--N, and NH_4^+-N concentrations and decreases the soil AP concentrations. The soil TN, SOC and TP concentrations showed a downward parabolic trend and the soil NO_3^--N, NH_4^+-N and AP concentrations showed an upward parabolic trend as the disturbance intensity increased in Luqu County and Maqu County, and these soil nutrients showed a theoretical threshold peak at 475(475 ± 90) burrow entrances per ha.

On the basis of these results, it can be concluded that an appropriate disturbance intensity of plateau pika is beneficial to the storage of soil carbon and nitrogen pools and the cycle of soil nitrogen in the QTP, as the available soil nitrogen (NO_3^--N and NH_4^+-N) can affect vegetation growth, nutrient supplies, and, especially, the colonization and reproduction of grasses or opportunistic plant species. When the disturbance intensity exceeds the threshold, the soil TN, SOC and TP concentrations are reduced because of the low vegetation cover and biomass, which will weaken the ecological function of alpine meadow. The results from this study will benefit our understanding of the role of plateau pika in the ecological environments of the QTP, and the data can be used to help formulate and implement constructive and management measures for plateau pika.

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