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Authors: Dorji, Tsechoe, Moe, Stein R., Klein, Julia A., , , and Totland, Ørjan

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Tsechoe Dorji*†

Stein R. Moe*

Julia A. Klein‡ and

Ørjan Totland*

*Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway
†Corresponding author: Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, 860000, Lhasa, Tibet Autonomous Region, China, tsechoedorji@itpcas.ac.cn
‡Department of Ecosystem Science and Sustainability, Colorado State University, Campus Delivery 1476, Fort Collins, Colorado 80523, U.S.A.

Abstract

Plant community properties such as species richness, evenness, and composition vary along environmental gradients. Arid and semi-arid ecosystems, such as the central Tibetan Plateau, are thought to be sensitive to changes in temperature and water availability, and also influenced by a long history of herbivore grazing. We used linear mixed effect models and Canonical Correspondence Analysis to explore how plant community properties varied along gradients of elevation, soil moisture, grazing intensity, solar radiation, ground surface roughness (ground concavity), and pika abundance in an alpine meadow ecosystem in central Tibet. We found that species richness increased with elevation. Species evenness increased with soil moisture at lower elevation, but decreased with soil moisture at higher elevation. Species composition was significantly associated with all environmental variables except solar radiation. The abundance of the dominant plant species, *K. pygmaea*, which is driven primarily by soil moisture, was also an important variable. We conclude that open patches (habitat), associated with elevation, number of pika burrows and surface roughness, and soil moisture and its effects on *K. pygmaea* were the most important environmental variables creating variation in plant community properties across this landscape.

Introduction

Plant community properties, such as species richness (number of species), evenness (abundance equality of species), and composition (identity of species), affect key ecosystem functions, including ecosystem stability (Tilman and Downing, 1994), resilience (Naeem et al., 2000), and total plant production (Aarssen et al., 2003). Plant community properties may vary with abiotic factors along latitude and elevation gradients (Rosenzweig, 1995). Changes in temperature and water availability along elevation gradients are thought to be the main underlying drivers of spatial variation in plant species richness (Pausas and Austin, 2001), evenness (Hegazy et al., 2007), and species composition (Semenova and van der Maarel, 2000). Species richness and evenness may peak at mid-level elevations (Colwell and Lees, 2000), although this pattern is highly scale-dependent (Pausas and Austin, 2001). Plant species richness may decrease linearly with elevation at large spatial scales (Stevens, 1992); however, Shimono et al. (2010) found a positive relationship between plant species richness and elevation across the Tibetan Plateau. Species richness may increase with water availability (Pausas and Austin, 2001). Hawkins et al. (2003) and O'Brien (1993), however, reported a positive quadratic (humped curve) relationship between species richness and water availability.

Grazing intensity is also important for plant community properties, particularly in grassland systems (Milchunas et al., 1988). However, the magnitude of grazing effects depends on ecosystem properties and the evolutionary grazing history (Milchunas et al., 1988). Ellis (1995) argued that in arid or semi-arid ecosystems, where interannual coefficient of variation in precipitation is greater than 33%, plant population dynamics and community properties are mainly controlled by abiotic factors, whereas in moister environments with less precipitation variation, plant community properties are more directly controlled by grazing. Milchunas et al. (1988) argued that in arid and semi-arid ecosystems with a long evolutionary history of grazing, plant community properties are less sensitive to grazing because species have become adapted to the grazing regime. Moreover, grasses and sedges may reproduce more than forbs under higher grazing intensity (Wu et al., 2011). Species richness and evenness may also show a hump-backed pattern along grazing intensity gradient (Roxburgh et al., 2004). However, such a pattern may also be scale-dependent (Milchunas et al., 1988).

Interactions between grazing intensity and abiotic conditions, such as temperature and moisture, may also be important in determining plant community properties in pastoral ecosystems (Rosenzweig, 1995). Klein et al. (2004) reported that experimental warming caused a rapid decrease in species richness on the eastern Tibetan plateau, an effect that was dampened by simulated grazing. Similar findings have been reported elsewhere (Post and Pedersen, 2008). Temperature may also interact with water availability in determining plant community properties (Richerson and Lum, 1980). Crimmins et al. (2011) found that the expected upward shift in species distribution with elevation under a warming scenario was dampened by water stress, thus causing an unexpected downward shift in species distribution due to an increased water deficit toward higher elevation. However, Lenoir et al. (2010) argued that a downward shift in species distribution is possibly an indirect response to both climate warming and anthropogenic habitat modification.

The Tibetan plateau, one of the most extensive alpine regions in the world, is thought to be particularly sensitive to global climate change (Klein et al., 2004). Moreover, as one of the largest pastoralist areas globally, the Tibetan plateau has been subjected

to, and thus experienced, large-scale landscape changes through a long history of animal husbandry practices (Miehe et al., 2011a, 2011b). However, the degree to which plant community properties respond to either climate or grazing may differ across the Tibetan plateau. Cincotta et al. (1992) argued that plant-herbivore interaction is the driving force of plant population dynamics on the eastern part of the Tibetan plateau, while Dorji et al. (2010) indicated that climatic variability is the principle driver of plant community properties on the northwestern part of the Tibetan plateau. While research has been conducted at large scales across the Tibetan Plateau (Shimono et al., 2010) and within experimental plots (Klein et al., 2004; Wang et al., 2009; Dorji et al., 2013b), there has been less work at an intermediate scale on how plant community properties may be controlled by abiotic environmental conditions and grazing intensity. Moreover, most plant ecological studies on the Tibetan Plateau are located on its eastern margin, and there is little information regarding plant community properties in the central Tibet grasslands.

In this study, we explore how livestock grazing and climate variability along elevation gradients have shaped plant community properties in central Tibet. In particular, we examine how species richness and evenness are associated with biotic and abiotic conditions at an intermediate landscape scale. We also relate environmental variables to life form (graminoids, shrubs, forbs, and cushion plants) abundances and species composition to assess how the distribution and abundance of different life forms and plant species change along environmental gradients. We hypothesize that temperature (using elevation as proxy) and soil moisture availability will explain most of the variation in species richness, evenness, and composition because our study site is a cold and semi-arid ecosystem with a long evolutionary grazing history (Milchunas et al., 1988).

Methods

STUDY SITE

The study site consisted of an area covering ~50 km² of south-, west-, and north-facing hillslopes in the Nam Tso region, Tibet, China (approximately 30°41.208 N to 30°44.579 N; 91°01.117 E to 91°04.590 E) at the base of the Nyenchen Tanglha mountain range. The mean annual temperature (MAT) is –0.6 °C. The mean annual precipitation (MAP) of Nam Tso region is 414.6 mm, with the majority of the precipitation occurring during the summer season, from June to September (Kang et al., 2011). MAT and MAP data for the Nam Tso region were based on five-year weather data at the Nam Co (Tso) Monitoring and Research Station for Multisphere Interactions, which is about 20 km northwest of our study site. The interannual coefficient of variation in precipitation is 26%, based on long-term weather data (1957–2011) of Baingoin weather station, about 100 km north of the study area. The long-term Baingoin weather data were obtained from the Global Historical Climatology Network website (National Climatic Data Center, 2012). The landscape is dominated by alpine meadow grassland, with *Kobresia pygmaea* C. B. Clarke as the dominant plant species in the region. The study site has a long history as summer pasture and currently harbors 869 yaks, 2370 sheep, 458 goats, and 26 horses belonging to 32 pastoral families, according to local administrative statistics. Yaks are semi free-ranging livestock. That is, herders release the yaks for grazing in the morning and herd them back to campsites in the evening, but do not follow the yak herds throughout the day. Yaks primarily graze on hillslopes that are close to the summer campsites, while sheep and goats are herded at farther distance from campsites, often with a big flock followed by a herder. In general, livestock grazing range is within 5 km radius from campsites (personal observation and communication with Dr. Nyima, who has conducted intensive interviews and field surveys on rangeland ecosystems and pastoralism in central Tibet, including in Nam Tso region). The study site was selected because it is an important summer grazing area for local pastoralists and represents typical summer pastures in the region, and because it has long been subjected to high abundance of pika (*Ochotona curzoniae* Hodgson), a small mammal regarded as a keystone species in the ecosystem (Smith and Foggin, 1999). Pikas have also been blamed for causing land degradation in the region, due to their grazing and burrowing (Li and Huang, 1995).

STUDY DESIGN

To study relationships between abiotic conditions, grazing intensity, and plant community properties, we selected seven hillslopes that are spatially independent across our study site, with an elevation range between 4800 to 5120 m. The hillslopes were selected from a distance without judging their vegetation and environmental conditions in order to avoid subjectivity in site selection. Each hillslope was stratified into five elevation zones (each of 60 elevation m) and three aspects (south-, west-, and north-facing slopes), yielding 15 sectors that correspond to each combination of elevation zone and aspect, in order to have equal sampling effort along the elevation and slope gradients. One 10 × 10 m plot was positioned in the center of each sector by visually identifying the center from the upper elevation limit of each sector. A maximum of 15 plots (one for each sector) were positioned on any hillslope, and each combination of elevation zone and aspect was replicated at least five times. Seventy-seven plots in total were positioned on the seven hillslopes across the study area. Because the hillslopes were spatially independent from each other and distributed over the whole study area, each plot located on a particular hillslope represented a unique combination of elevation and aspect, and the distance between two adjacent plots was at least 80 m, we regarded the sampling plots to be spatially independent. In each sampling plot, five quadrats of 1 × 1 m were systematically located, with one in each corner and one in the center of the plot.

DATA COLLECTION

We sampled plant species in each quadrat from 20 July to 6 August in 2009. Because of the relatively low plant cover in the region, we used a slightly modified version of the point intercept method (Jonasson, 1988), by evenly distributing 100 pins (less than 1 mm diameter) in the quadrat frame and recording all plant species that were present within 1 cm radius around the pin for a better representation of particularly rare species. Thus, species richness per quadrat was the number of species that was represented within 1 cm radius from the 100 pins, while plant species abundance was calculated as the number of circles within which each plant species was present. The species richness for each plot was the number of species per plot. The species evenness was calculated as follows (Alatalo, 1981):

$$\text{Evenness} = [(\textstyle\sum p i^2)^{-1} - 1]/[\exp(-\textstyle\sum p i \log_e p_1) - 1] \qquad (1)$$

where p_i is the proportion of individuals belonging to the *i*th species and $\sum$ denotes the summation from $i = 1$ to $i = s$, with s

being the number of species in the sample. We used this equation to calculate evenness, because it makes the estimation less sensitive to sample size (Alatalo, 1981). Evenness and diversity were highly correlated ($r = 0.79$, $p < 0.001$). We chose two components of species diversity, species richness and evenness, rather than species diversity itself in this study, because it is ecologically simpler to interpret the two components separately (Stirling and Wilsey, 2001). Plants not identified in the field were taken to the University of Bergen, Norway, for identification. We classified plant species into functional groups using life form, which includes graminoids, shrubs, cushion plants, and forbs. See Appendix Table A1 for a list of species and their corresponding distribution range and abundance across the study area.

Predictor variables considered were solar radiation index, elevation, soil moisture, pika burrows, surface roughness, and grazing intensity. Solar radiation index (SRI) for each plot was calculated by using the formula suggested by Keating et al. (2007) as follows:

$$SRI = \cos(latitude)\cos(slope) + \ln(latitude)\sin(slope)\cos(aspect) \quad (2)$$

where *latitude* and *slope* were in unit of degrees, while *aspect* was calculated as original aspect data minus 180. Latitude, longitude, and elevation data were obtained for each sampling plot using a global positioning system (GPS) devise. We used a standard compass to measure aspect and slope angle at the center of each plot.

To measure soil moisture content, five soil samples ($5 \times 5 \times 10$ cm core) were taken in each sampling quadrat after the vegetation measurements were completed in each plot. The five soil samples taken from one plot were mixed and sealed into one plastic bag on-site. Gravimetric soil moisture content for each plot was measured by weighing the soil sample before and after drying the soil at 60 °C for 48 hours. Daily precipitation data (15 July to 15 August 2009) were obtained from the Nam Co (Tso) Monitoring and Research Station. Since the mean soil moisture on each date of measurement corresponded to the total precipitation amount that occurred within two days before each date of measurement, we adjusted the soil moisture data, in order to avoid the impact of rainfall on soil moisture. First, we used total precipitation values within two days before each date of the field soil moisture measurements to create a calibration datum on each date of measurement. The calibration data, therefore, consisted of 17 values with 1 value for each date of measurement. Next, we standardized (0 mean with 1 standard deviation) the soil moisture (which consisted of 77 values with 1 for each plot) and calibration data, because they were in different scales (soil moisture was in percentage scale and the calibration data were in mm). Finally, we obtained the adjusted soil moisture data of each plot by subtracting standardized values (z-scores) of the calibration data on each date of measurement from z-scores of soil moisture of all plots that were measured on the same day.

Surface roughness data were obtained by moving a stretched string on the surface of each quadrat to detect concavo-convex surface and then measuring the deepest concavo-convex surface of each quadrat using a ruler. We also estimated the grazing intensity of and disturbance from pika in each plot (Dorji et al., 2013a).

STATISTICAL ANALYSES

We used quadrat level data (consisting of 385 quadrats within 77 plots) in our analyses. Since the variables have different measurement scales, we standardized them prior to analyses in order to compare the effect size of each explanatory variable on each response variable We examined a correlation matrix between explanatory variables (Quinn and Keough, 2002). The highest correlation coefficient was –0.28 (between grazing intensity and elevation).

To explore how each response variable was related to environmental and grazing variables, we used a set of linear mixed effects models (LME) with plot as a random variable and linear and quadratic (second order) terms and interaction terms of environmental and grazing variables as explanatory variables against each response variable (species richness, evenness, and abundances of graminoids, forbs, shrubs, cushion plants, and *K. pygmaea*—the most abundant species). We used LME models to take into account the variation among quadrats in our analyses while dealing with pseudoreplication among the five quadrats within each plot. Since quadrats within each plot were not independent, we defined plot as a random variable in the LME models (Crawley, 2007). The quadratic terms were used because the response variables could exhibit unimodal relationships to the explanatory variables, depending on ecosystem properties (Rahbek, 1995; Vetaas and Grytnes, 2002). We used backward elimination to find the best model for each response variable by removing the least significant terms, starting with interaction terms, followed by quadratic and then linear terms (Crawley, 2007). The interaction and quadratic terms used in the LME models followed Crawley (2007). We used the Akaike information criterion (AIC) and likelihood ratio tests to compare between models to identify the final best models for each response variable (Crawley, 2007). We also investigated how each response variable in 5 m² (combining data from five quadrats of 1 m² within each combination of elevation and aspect zone in our study area) related to environmental and grazing variables using generalized linear model (GLM) (Appendix Figs. A1–A6). A series of diagnostic procedures (error distribution, data normality, and outliers) were conducted to validate the model adequacy and performance (Appendix Fig. A7). The analyses and their relevant plots were generated using package "lme4" (Douglas Bates et al., 2012) and "nlme" (Jose Pinheiro et al., 2012) in R 2.13.2. (R Development Core Team, 2012) .

We used canonical correspondence analysis (CCA) with CANOCO 4.5 (ter Braak and Šmilauer, 2002) to examine how plant species composition was associated with the measured environmental and grazing variables. We examined the significance of the first CCA axis, the full model, and each environmental and grazing related variable by using 499 Monte Carlo permutations. The highest variance inflation factor value for the predictor variables in the CCA was 1.42, indicating low collinearity among predictor variables.

Results

SPECIES RICHNESS AND EVENNESS

Variation in species richness was significantly and best explained by elevation, with species richness increasing with elevation (Table 1). Soil moisture also marginally significantly explained variation in species richness (Table 1). Species evenness had a unimodal relationship with elevation (Fig. 1, part a), while the relationship between evenness and soil moisture differed across the elevation gradient, as indicated by a significant interaction between soil moisture and elevation (Table 2). Evenness had a positive relationship with soil moisture at lower elevations (i.e., below 4890 m), but this pattern gradually changed as elevation increased, and there was a strong negative relationship between soil moisture and evenness at higher elevation (Fig. 1, part b). The likelihood

TABLE 1

Standardized estimates of linear mixed-effect models (with plot as random variable) and corresponding delta of Akaike information criteria values (ΔAIC), comparing the final model and weight of corresponding model against the full model to present relationships between species richness and explanatory variables at Nam Tso, Tibet, China, in 2009. DF stands for degrees of freedom. Only a few candidate models are presented in this table for illustration purposes.

Parameters	Models					
	Final (6)	5	4	3	2	Full (1)
(Intercept)	0.00	0.00	0.00	0.00	0.34	0.35
Solar radiation index	—	—	—	–0.04	–0.04	–0.04
Solar radiation index^2	—	—	—	—	–0.11	–0.14
Elevation	**0.28**	**0.23**	**0.31**	**0.30**	**0.28**	**0.30**
Elevation^2	—	—	—	—	–0.10	–0.06
Grazing intensity			–0.06	–0.06	–0.05	–0.05
Grazing intensity^2	—	—	—	—	–0.04	–0.05
Pika burrows			0.14	0.14	0.16	0.18
Pika burrows^2	—	—	—	—	–0.05	–0.07
Surface roughness	—	—	0.07	0.06	0.06	0.05
Soil moisture	–0.12		*–0.14*	*–0.15*	*–0.12*	*–0.17*
Soil moisture^2	—	—	—	—	–0.03	–0.01
Elevation: grazing intensity	—	—	—	—	—	0.02
Elevation: soil moisture	—	—	—	—	—	–0.09
Soil moisture: grazing intensity	—	—	—	—	—	0.03
DF	5	4	8	9	14	17
ΔAIC	0.00	0.56	0.67	2.53	6.79	11.25
Weight	0.36	0.27	0.26	0.10	0.01	0.00

"^{2}" At end of variables indicates quadratic terms.

":"At end of variables indicates interaction terms.

Bold and italic numbers indicate corresponding variables were significant at $p < 0.05$ and 0.10, respectively.

"—" indicates variables that were not included in corresponding models.
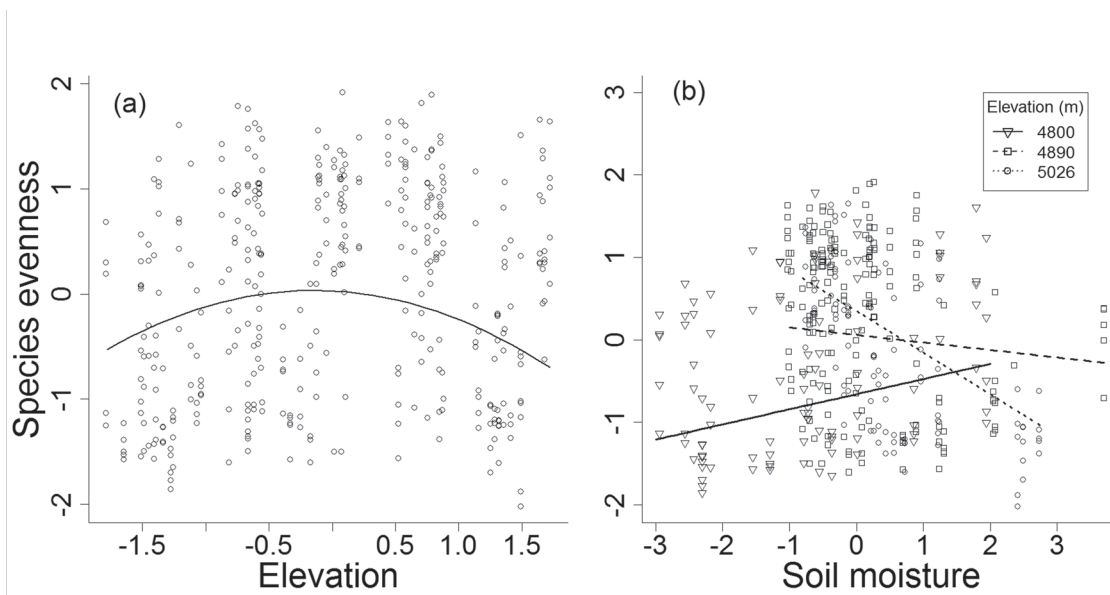

FIGURE 1. Graphs illustrating significant quadratic and interaction terms involved in best subset linear mixed effect (LME) model for species evenness at Nam Tso, Tibet Autonomous Region of China, in 2009. Regression lines were based on estimates of parameters in the LME model. The explanatory variables used in the full model to derive the best subset models include first and second order terms for elevation, soil moisture, grazing intensity, pika burrow, solar radiation index, and surface roughness, and interaction terms between grazing intensity, elevation, and soil moisture.

TABLE 2

Standardized estimates of linear mixed-effect models (with plot as random variable) and corresponding delta of Akaike information criteria values (ΔAIC) comparing the final model and weight of corresponding model against the full model to present relationships between species evenness and explanatory variables at Nam Tso, Tibet, China, in 2009. DF stands for degrees of freedom. Only a few candidate models are presented in this table for illustration purposes.

Parameters	Final (6)	5	4	3	2	Full (1)
(Intercept)	0.31	0.31	0.33	0.33	0.27	0.27
Solar radiation index	—	—	0.11	0.11	0.12	0.12
Solar radiation index^2	—	—	—	—	0.04	0.04
Elevation	**0.21**	**0.20**	**0.20**	**0.20**	**0.25**	**0.24**
Elevation^2	**–0.21**	**–0.20**	**–0.23**	**–0.23**	**–0.27**	**–0.25**
Grazing intensity	—	–0.05	–0.05	–0.05	–0.05	–0.05
Grazing intensity^2	—	—	—	—	0.03	0.03
Pika burrows				–0.05	–0.01	–0.01
Pika burrows^2	—	—	—	—	–0.04	–0.04
Surface roughness	—	—	—	0.02	0.01	0.01
Soil moisture	**–0.28**	**–0.27**	**–0.25**	**–0.25**	**–0.30**	**–0.30**
Soil moisture^2	—	—	—	—	0.05	0.05
Elevation: grazing intensity	—	—	—	—	—	0.04
Elevation: soil moisture	**–0.27**	**–0.27**	**–0.27**	**–0.27**	**–0.31**	**–0.33**
Soil moisture: grazing intensity	—	—	—	—	—	0.00
DF	7	8	10	11	15	17
ΔAIC	0.00	1.12	2.73	4.70	9.48	12.98
Weight	0.52	0.30	0.13	0.05	0.01	0.00

"^{2}" At end of variables indicates quadratic terms.
":" At end of variables indicates interaction terms.
Bold and italic numbers indicate corresponding variables were significant at $p < 0.05$ and 0.10, respectively.
"—" Indicates variables that were not included in corresponding models.

test showed that the best model did not significantly differ from the second most parsimonious model for species evenness ($F = 0.27$, $p = 0.60$). Grazing intensity, surface roughness, pika burrows, and solar radiation index did not significantly explain variation in species richness and evenness.

LIFE-FORM ABUNDANCE

In contrast to species evenness, graminoid abundance was lowest at mid-elevation (Fig 2, part a), and grazing intensity was also significant in explaining variation in graminoid abundance, with highest at intermediate grazing intensity (Fig. 2, part b). Graminoid abundance increased with soil moisture across the elevation gradient, and it was highly significant only at higher elevations, not at lower elevations (Fig. 2, part c).

Forb abundance demonstrated a unimodal relationship with elevation (Fig. 3, part a), while the relationship between forb abundance and grazing intensity differed across the elevation gradient (Fig. 3, part b). Forb abundance had negative relationship with grazing intensity at lower elevation (i.e., below 4890 m), but this pattern gradually changed as elevation increased, and there was a positive relationship between forb abundance

and grazing intensity at higher elevation (e.g., 5026 m) (Fig. 3, part b).

Shrub abundance also varied along the soil moisture gradient, but the relationship differed across the elevation gradient (Fig. 3, part d). Shrub abundance had a positive relationship with soil moisture at lower elevations (i.e., below 4890 m), but this pattern gradually changed as elevation increased, and there was a negative relationship between soil moisture and shrub abundance at higher elevation (Fig. 3, part d). Shrub abundance also demonstrated a unimodal relationship with the number of pika burrows (Fig. 3, part c).

SPECIES COMPOSITION

The CCA model for species composition was highly significant ($F = 9.06$, $P < 0.01$), and explained 13% of the total variation (sum of all canonical eigenvalues per sum of all eigenvalues) in plant species composition. In this model, the first CCA axis, which was associated with grazing intensity and soil moisture (correlation coefficients were 0.38 and 0.35, respectively), was highly significant ($F = 32.47$, $P < 0.01$). All six variables included in the model were highly significant in ex-
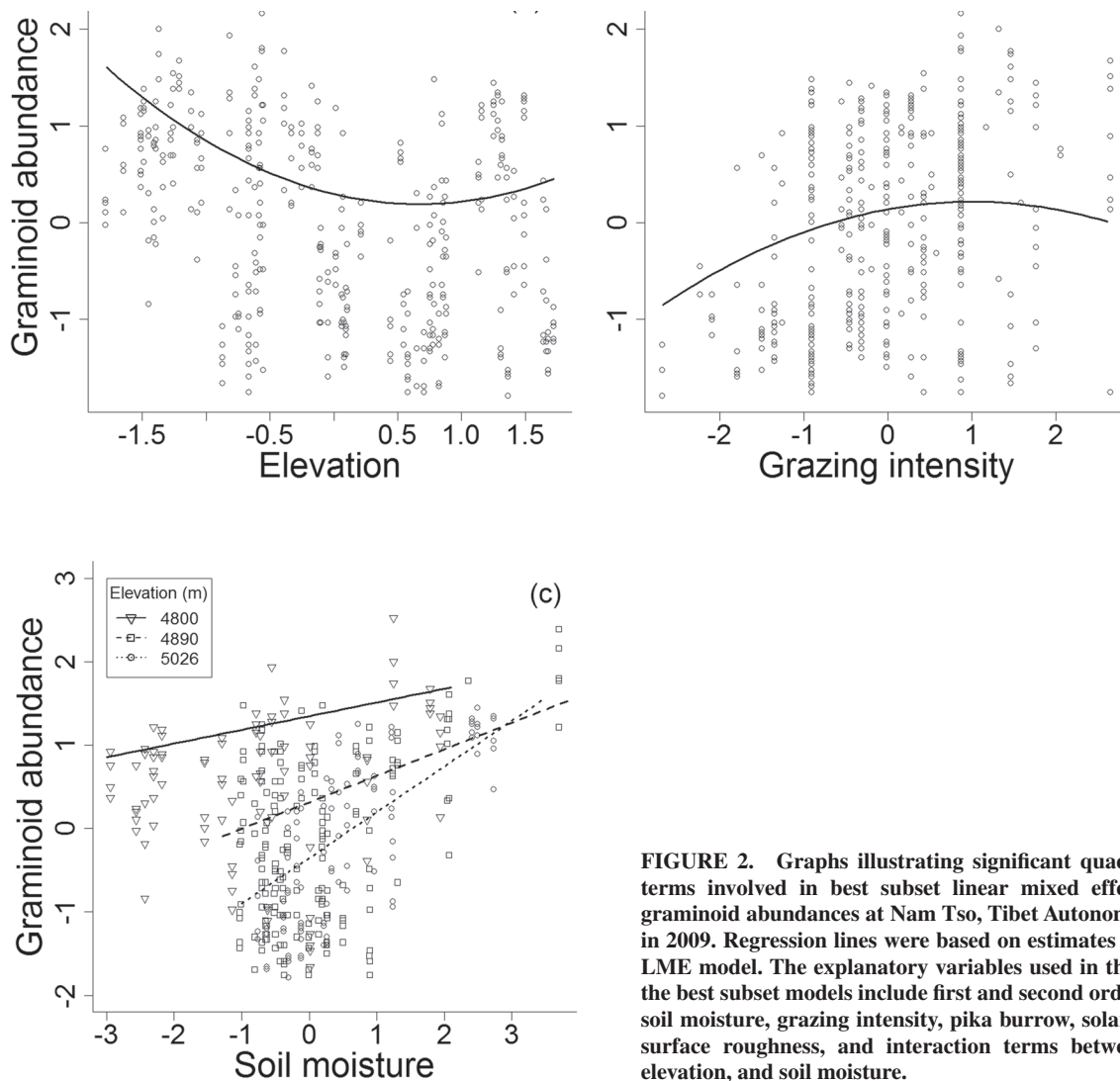
FIGURE 2. Graphs illustrating significant quadratic and interaction terms involved in best subset linear mixed effect model (LME) for graminoid abundances at Nam Tso, Tibet Autonomous Region of China, in 2009. Regression lines were based on estimates of parameters in each LME model. The explanatory variables used in the full model to derive the best subset models include first and second order terms for elevation, soil moisture, grazing intensity, pika burrow, solar radiation index, and surface roughness, and interaction terms between grazing intensity, elevation, and soil moisture.

plaining variation in species composition and abundance ($P <$ 0.01), except for solar radiation.

We recorded 93 plant species belonging to 63 genera. Graminoid species *K. pygmaea*, *C. incurva*, *C. moocroftii,* and *P. hirtiglumis* were the dominant species in the study area (Appendix Table A1). Species of Fabaceae, Rosaceae, Caryophyllaceae, and Asteraceae were also common. In total, 11 graminoids, 4 cushion plants, 4 shrub species, and 74 forb species were found. No overall distribution patterns occurred for graminoids, even though there are species-specific preferences toward certain environmental gradients (Fig. 4, part a). The most dominant species, *K. pygmaea,* was positioned close to the center of the CCA diagram with slightly above-average grazing intensity, and pika burrows, but below-average surface roughness and elevation (Fig. 4, part a). *K. pygmaea* abundance increased with soil moisture at higher elevation, but decreased with soil moisture at lower elevation (Fig. 5, part b). Shrubs were mainly distributed at lower soil moisture and grazing intensity, and below average surface roughness (Fig. 4, part b). *Potentilla fruticosa* L., the most common shrub species in the area, was distributed at below-average soil moisture and grazing

intensity, and slightly above-average elevation (Fig. 4, part b). Cushion plant species occurred at above-average elevation and below-average soil moisture and grazing intensity, although one unidentified *Arenaria* species tended to favor higher grazing intensity (Fig. 4, part c). There was no specific overall distributional pattern for forbs along environmental gradients (Fig. 4, part d).

Discussion

SPECIES RICHNESS AND EVENNESS

Our results indicate that patterns of species richness and evenness were significantly associated with elevation and soil moisture, as we hypothesized and also as reported elsewhere in arid alpine ecosystems with a long evolutionary grazing history (Sala et al., 2000). Species richness increased linearly with elevation. This is not consistent with other studies where species richness decreases monotonically (Stevens, 1992) or shows a hump-backed pattern along elevation gradients (Rahbek, 1995; Vetaas and Grytnes, 2002). Our elevation gradient only covered 300 m, but the posi-
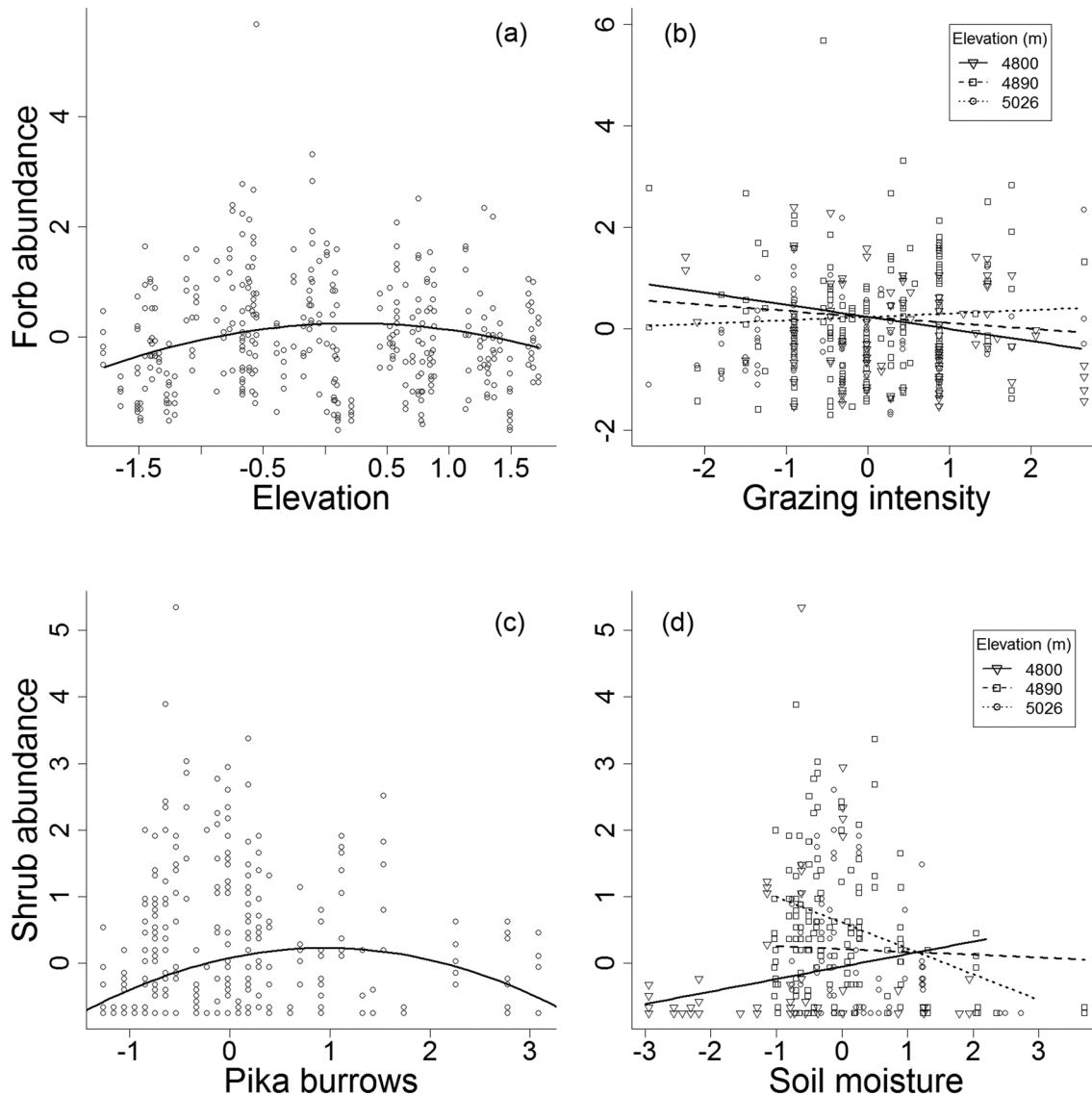
FIGURE 3. Graphs illustrating significant quadratic and interaction terms involved in best subset linear mixed effect model (LME) for (a and b) forb and (c and d) shrub abundances at Nam Tso, Tibet Autonomous Region of China, in 2009. Regression lines were based on estimates of parameters in each LME model. The explanatory variables used in full model to derive best subset models include first and second order terms for elevation, soil moisture, grazing intensity, pika burrow, solar radiation index, and surface roughness, and interaction terms between grazing intensity, elevation, and soil moisture.

tion of the gradient (4800–5105 m) was well above the elevation at which the maximum number of species occurred in other alpine regions located in a similar latitudinal range (Vetaas and Grytnes, 2002; Tang et al., 2006; Wang et al., 2007). Thus, we would expect a decreasing rather than increasing trend of species richness with altitude. Shimono et al. (2010) reported a weak linear increase in species richness with elevation across the Tibetan plateau, but they did not propose a mechanism behind their result. Qiong et al. (2011) also reported an increasing pattern of species richness along an elevation gradient in central Tibet using 1 m² quadrats. However, this trend was reversed when they increased quadrat size to 6 m² (combining data from six quadrats of 1 m² within same elevation zone; each zone spanned 25 elevation m). They argued that such a pattern could be attributed to grazing pattern of livestock (mainly yaks) in the region, but suggested no definitive mechanisms. We

also investigated how species richness in 5 m² (combining data from five quadrats of 1 m² within each combination of elevation and aspect zone in our study area) related to elevation, but found no trend of decreasing species richness with elevation (Appendix Fig. A1). Rahbek (1995) proposed that slope steepness, and thereby disturbance, may affect the altitudinal patterns of species richness, and that open patches (bare ground) may provide new habitats for opportunistic species (Li et al., 2002). Callaway et al. (2002) indicated that facilitation occurs at higher elevations, which may also promote higher species richness at higher elevation. We often observed patches of fragmented *K. pygmaea* mats that were sparsely vegetated by other species (often forbs and shrubs) on upper hills with steep slopes in our study area. Indeed, the amount of open ground increased significantly with elevation ($r = 0.43$, $p < 0.001$), which was highly correlated with slope steepness ($r = 0.60$, $p <$
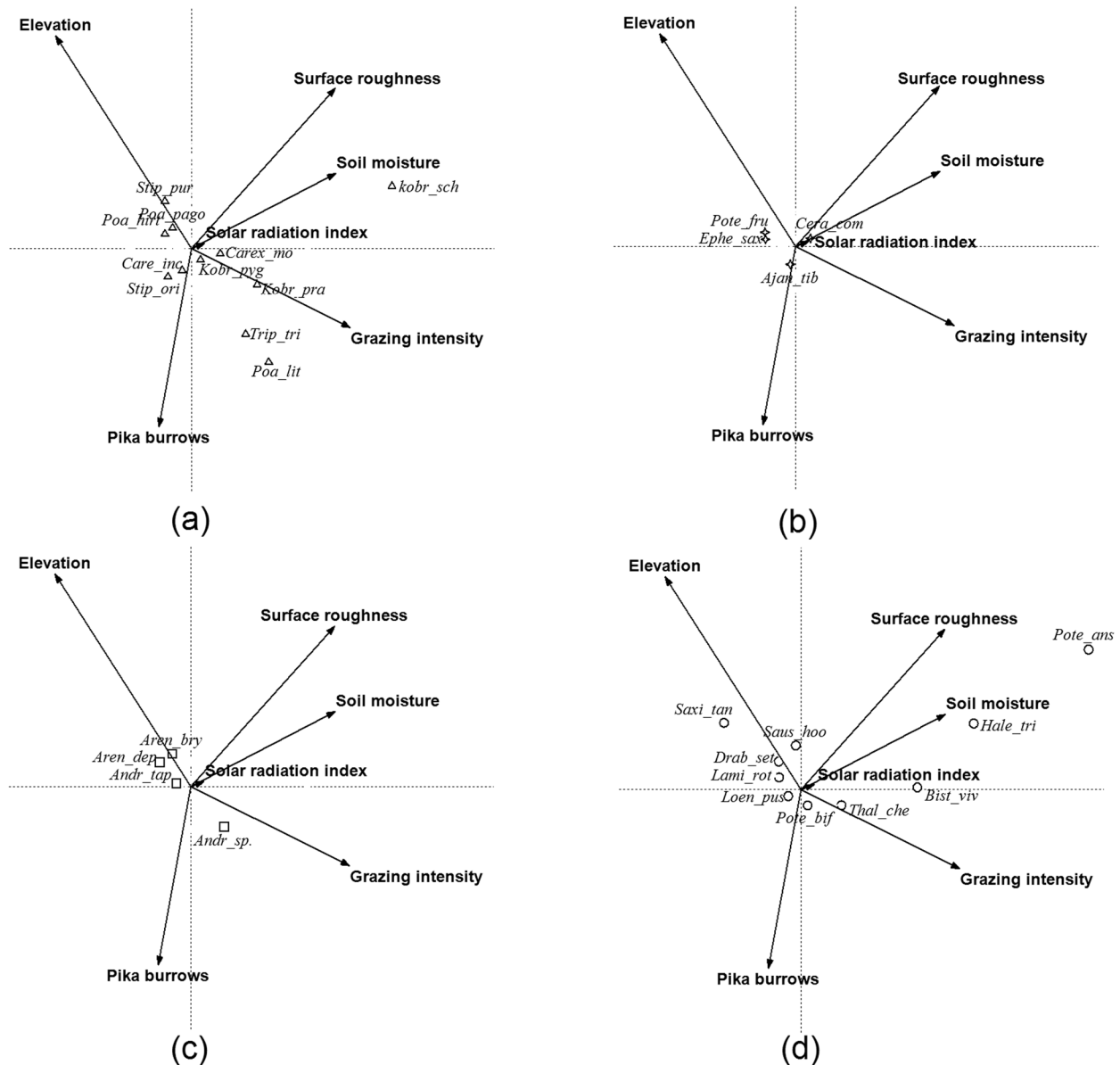
FIGURE 4. Canonical correspondence analysis (CCA) biplots for (a) graminoids, (b) shrubs, (c) cushion plants, and (d) forb species with above 3% fit at Nam Tso, Tibet Autonomous Region of China, in 2009. Lines with arrowhead represent environmental and grazing related variables. For comparison purposes, all plots were based on same CCA result to illustrate the position of each species belonging to different life forms on the same CCA diagram. SRI represents solar radiation index. Coded species names correspond to the abbreviations in Appendix Table A1.

0.001). Thus, it is possible that steeper slope at higher elevations increases erosion, which creates open patches for opportunistic species, and thereby contributes to the increased species richness with elevation in our study area.

Species evenness decreased with increasing soil moisture at higher elevations, whereas it increased with soil moisture at lower elevations. Cerabolini et al. (2010) argued that in communities with very low species evenness (i.e., having one or a few species with a very high relative abundance), the variation in community evenness may to a large extent be driven by the spatial variation in the abundance of the dominant species. In our study area, *K. pygmaea* is highly dominant throughout the region. Thus, it is likely that the variation in species evenness was mainly driven by the

variation in population density of *K. pygmaea*. Indeed, there is a strong negative relationship between *K. pygmaea* abundance and species evenness ($r = –0.80$, $p < 0.001$), and the pattern of *K. pygmaea* abundance was exactly opposite to that of species evenness along soil moisture and elevation gradients (Fig. 5, parts a and b).

Grazing intensity was less important for species richness and evenness than habitat availability (represented by elevation) and soil moisture. This is surprising since grazing has been suggested by Miehe et al. (2011b) to be particularly important for plant community properties in alpine meadow ecosystems on the Tibetan plateau, even though they also acknowledged the importance of local climate in the region. Our grazing intensity measure was a one-time measurement. Thus, it may not reflect the long-term his-
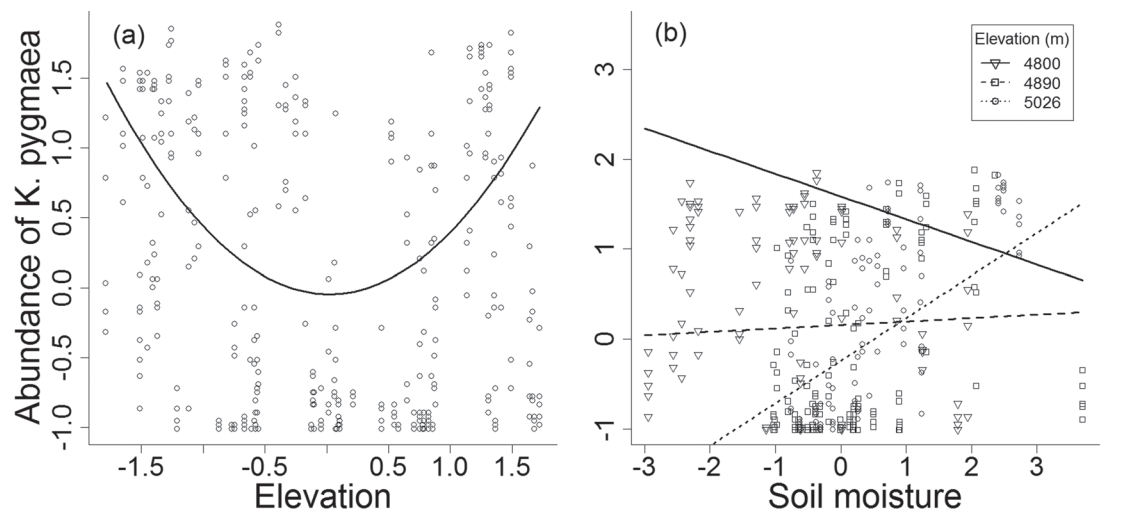
FIGURE 5. Graphs illustrating significant quadratic and interaction terms involved in best subset linear mixed effect model (LME) for abundance of *Kobresia pygmaea* C. B. Clarke. Regression lines were based on estimates of parameters in the LME model. The explanatory variables used in full model to derive best subset models include first and second order terms for elevation, soil moisture, grazing intensity, pika burrow, solar radiation index, and surface roughness, and interaction terms between grazing intensity, elevation, and soil moisture.

toric grazing intensity in the region. However, in sites with a long evolutionary history of grazing, such as our study area, the system may be well-adapted to grazing and therefore could be highly resilient and relatively insensitive to grazing. This phenomenon has been documented on, for example, the shortgrass steppe ecosystem in North America (Milchunas et al., 1988). It is also possible that plant population dynamic and community properties are mainly controlled by climate variability, such as precipitation, rather than grazing intensity, as suggested for other arid and semi-arid ecosystems in Africa (Ellis, 1995) and the northwestern Tibetan plateau (Dorji et al., 2010). In fact, this appears to occur in our study where the variation in species richness and evenness was mainly associated with soil moisture.

LIFE-FORM ABUNDANCE AND SPECIES COMPOSITION

Plants with contrasting life forms are also expected to respond differently to environmental change, due to differences in their morphological and physiological adaptations (Semenova and van der Maarel, 2000). We found that shrub abundance was significantly associated with elevation, soil moisture, and pika burrows (habitat disturbances by pika). The CCA analyses also indicated that shrubs were mainly distributed at below-average soil moisture. These results are consistent with a hypothesis where shrubs are expected to be generally drought resistant with deep root systems, enabling them to extract water from deeper soils (Jackson et al., 1996) and where habitat heterogeneity created by pika burrows may facilitate shrub expansion due to a reduced competition from the dominant graminoid species, *K. pygmaea*. We also found that *Potentilla fruticosa,* the dominant shrub species in our study area, mainly occurred at below-average soil moisture, where its deeper roots may be advantageous, and at above-average elevation, where its rooting system may enhance vegetation stabilization on steeper, eroding slopes.

Spatial variation in species composition was best explained by elevation and soil moisture, followed by number of pika burrows, small-scale surface roughness, and grazing intensity. The impor-

tance of elevation for species composition indicates that the system is either sensitive to even small changes in temperature, as we would expect in high-elevation alpine ecosystems (Körner, 2003), or to the availability of open patches (new habitats for plants) associated with the elevation gradient, as discussed above. We suggest that long-term multiple seasonal monitoring of temperature along the elevation gradients is needed to identify causal mechanisms for the observed patterns of plant species composition in the region. Species composition and abundance were also significantly different along the soil moisture gradient, even though most of the species in our study area are distributed at the drier part of the soil moisture gradient, and thus appear to be drought resistant. Species that often dominate marshland ecosystems, such as *K. schoenoides* and *Potentilla anserina* L., occurred mainly at the wetter end of the soil moisture gradient, while those that are relatively deep-rooted (mainly shrubs) were located at lower soil moisture, as we discussed previously.

Small-scale heterogeneity in habitat disturbances seem to play an important role in structuring species composition in our study area, because both surface roughness and pika burrows (index of habitat disturbances by pika) significantly explained variation in species composition and abundances. Such patterns are conceivable because opportunistic species may establish at low density in highly disturbed areas (Callaway et al., 2002) (i.e., plots with a high level of surface roughness or higher number of pika burrows), leading to a distinctive small-scale mosaic of species across the disturbance gradient (Marcante et al., 2009). Nevertheless, these results were inconsistent in that neither surface roughness nor pika burrows significantly explained variation in species richness and evenness. These results indicate that different community properties, such as species richness, evenness, and composition may respond differently to small-scale heterogeneity in habitat disturbances. Grazing intensity was also significant in explaining species composition and abundances. The fact that grazing animals are selective, and some plants may be more tolerant to grazing than others (Coppock et al., 1983), may have resulted in a different species composition along the grazing intensity gradient.

Conclusion

We conclude that changes in plant species richness, evenness, and composition were mainly associated with open habitat patches, associated with elevation, number of pika burrows, surface roughness, and soil moisture in our study system. Furthermore, the abundance of the dominant plant species, *K. pygmaea*, may determine patterns of species richness, evenness, and composition along environmental gradients. Thus, any changes in abundance of *K. pygmaea* may alter species richness, evenness, and composition. The abundance of *K. pygmaea* is likely driven primarily by soil moisture conditions. Thus, future changes in precipitation may have large effects on species richness, evenness, and composition, partly via indirect effects on the dominant *K. pygmaea*.

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APPENDIX

TABLE A1

Species name, abbreviations, number of plots (total 77 plots of 10 × 10 m), and quadrats (total 385 quadrats of 1 × 1 m) in which each species occurred, mean abundance of each species in each quadrat, elevation range and aspect (N = north; S = south; W = west) of each species found in all plots in Nam Tso region, central Tibet Autonomous Region of China (30°41.208′N°30°44.579′N; 91°01.117′E°91°04.590′E) in summer 2009. Plant species are listed from the most abundant to the least abundant within each life form (shrubs, cushion plants, graminoids, and forbs). Abbreviations of each species correspond to species names displayed in Figure 3.

Species	Abbreviation	Plots	Quadrats	Abundance	Elevation	Aspect
Shrubs						
Potentilla fruticosa Linn	Pote_fru	55	209	13.37	4812–5104	N,W,S
Ajania tibetica (Hook. f. et Thoms. ex C. B. Clarke) Tzvel	Ajan_tib	21	52	3.65	4800–5073	N,W,S
Ephedra saxatilis Royle ex Florin	Ephe_sax	4	8	3.25	4897–5026	S
Ceratoides compacta (Losinsk) Tsien et C.G.Ma	Cera_com	2	3	1.00	4946–4962	S
Cushion plants						
Androsace tapete Maxim	Andr_tap	56	199	4.75	4800–5104	N,W,S
Arenaria bryophylla Fernald	Aren_bry	49	160	2.97	4800–5104	N,W,S
Arenaria pulvinata Edgew	Aren_dep	47	132	2.57	4858–1054	N,W,S
Androsace sp	Andr_sp.	1	1	1.00	4907	W
Graminoids						
Kobresia pygmaea C. B. Clarke	Kobr_pyg	70	323	37.77	4800–5104	N,W,S
Carex incurva Lightf	Care_inc	15	45	23.84	4858–5030	N,W,S
Kobresia schoenoides (C. A. Meyer) Steudel	kobr_sch	31	73	13.52	4800–5097	N,W,S
Carex moocroftii Falc. ex Boott	Carex_mo	69	299	9.39	4800–5104	N,W,S
Poa hirtiglumis var. Hook. *f.* var. *nimuana* (C. Ling) Soreng et G. Zhu	Poa_hirt	67	245	7.64	4800–5104	N,W,S
Poa litwinowiana Ovcz	Poa_lit	2	4	7.25	4858–4897	N
Poa pagophila Bor	Poa_pago	70	320	6.96	4800–5104	N,W,S
Tripogon trifidus Munro ex Hook	Trip_tri	6	7	3.43	4858–5072	W,N
Stipa purpurea Griseb	Stip_pur	29	64	2.44	4902–5104	N,W,S
Kobresia prainii Kukenth	Kobr_pra	7	10	2.40	4858–5097	W,N
Stipa orientalis Trin	Stip_ori	6	6	1.33	4846–5016	N,W,S
Forbs						
Leontopodium pusillum (Beauv) Hand.-Mazz	Loen_pus	69	300	8.08	4800–5104	N,W,S
Potentilla saundersiana Royle	Pote_sau	72	306	7.81	4800–5104	N,W,S
Saussurea taraxacifolia Wall. ex DC	Saus_tar	11	30	7.47	4800–5063	N,W,S
Lomatogoniopsis alpina T. N. Ho et S. W. Liu	Loma_oni	1	1	7.00	4890	S
Dracocephalum heterophyllum Benth	Drac_het	2	2	7.00	4800–4824	W
Saussurea hookeri C. B. Clarke	Saus_hoo	12	36	6.25	4961–5077	N,W,S
Eritrichium sp.	Erit_sp.	5	5	6.00	4897–5100	S,W
Aster flaccidus subsp. Bunge subsp. *flaccidus* Onno	Aste_fla	55	192	5.86	4800–5104	N,W,S
Astragalus rigidulus Benth. ex Bunge	Astr_rig	65	244	5.28	4800–5104	N,W,S
Polygonum sp.	Poly_sp.	3	4	5.25	4906–5020	S,W
Parnassia chinensis Franch	Parc_chi	2	3	4.67	4824–4962	S
Thalictrum chelidonii DC	Thal_che	33	92	4.51	4800–5097	N,W,S
Cortia depressa (Don) Norm	Cort_dep	6	7	4.43	4800–5031	N,W,S

Species	Abbreviation	Plots	Quadrats	Abundance	Elevation	Aspect
Potentilla bifurca Linn	Pote_bif	52	186	4.04	4800–5104	N,W,S
Cortiella sp.	Cort_sp	1	5	3.80	5073	S
Potentilla anserina Linn	Pote_ans	1	2	3.50	4906	S,W
Polygonum sibiricum Laxm	Poly_sib	1	3	3.33	5066	W
Lamiophlomis rotate (Benth) Kudo	Lami_rot	61	219	3.10	4800–5104	N,W,S
Oxytropis falcata Bunge	Oxyt_moo	5	6	3.00	4897–5005	N,W,S
Polygonum viviparum Linn	Bist_viv	6	11	3.00	4812–5055	N,W,S
Polygonum sp.	Poly_sp.	2	2	3.00	4956–5023	N.S
Lancea tibetica Hook. f. et Thomson	Lanc_tib	33	70	2.99	4826–5099	N,W,S
Stellaria decumbens var. Edgew var. *polyantha* Edgew et Hook	Stel_dec	15	28	2.89	4800–5030	N,W,S
Dilophia fontana var. Maxim	Dilo_fon	4	3	2.67	4800–5005	N.S
Saxifraga tangutica Engl	Saxi_tan	16	34	2.59	4960–5104	N,W,S
Urtica hyperborea Jacq. ex Wedd	Urti_hype	1	2	2.50	5031	N
Artemisia sp.	Arti_sp.	5	13	2.46	4904–5104	S,W
Sibbaldia adpressa Bge	Sibb_adp	22	40	2.43	4800–5023	N,W,S
Unknown	unkonwn	2	3	2.33	4858–5030	S,W
Pedicularis roylei Maxim	Pedi_roy	3	6	2.33	4800–5084	N,W,S
Cortiella cortioides (C. Norman) M. F. Watson	Cort_cor	10	15	2.33	4904–5097	N,W,S
Stellaria subumbellata Edgew	Stel_sub	4	6	2.33	4888–4897	N,W,S
Halerpestes tricuspis (Maxim) Hand.-Mazz	Hale_tri	2	4	2.25	4850–5053	W
Gentiana sp.	Gent_sp.	18	33	2.21	4812–5069	N,W,S
Anemone obtusiloba subsp. D. Don subsp. *megaphylla* W. T. Wang	Anem_obt	1	1	2.00	5073	S
Comastoma sp.	Coma_sp.	1	2	2.00	4865	S
Microulia sp.	Micr_sp.	53	98	1.96	4824–5104	N,W,S
Taraxacum leucanthum Ledeb	Tara_leu	35	60	1.93	5066–5104	N,W,S
Draba setosa Royle	Drab_set	58	136	1.88	4800–5104	N,W,S
Taraxacum sp.	Tara_sp.	5	8	1.88	4858–5028	W,N
Pedicularis cheilanthifolia Schrenk	Pedi_che	19	26	1.85	4905–5100	N,W,S
Aconitum pendulum Busch	Acon_pen	2	6	1.83	4907–5100	W,N
Hypecoum leptocarpum Hook. f. et Thoms	Hyper_lep	7	12	1.83	4907–5084	N,W,S
Corydalis crispa Prain	Cory_cri	34	46	1.72	4800–5104	N,W,S
Ranunculus brotherusii Freyn	Renu_bro	24	38	1.58	4800–5099	N,W,S
Unkown 2	unknown2	18	22	1.50	4824–5097	N,W,S
Corydalis scaberula Maxim	Cory_sca	2	2	1.50	5073.00	S
Gentiana micantiformis Bur	Gent_mic	16	22	1.45	4946–5084	S,W
Saxifraga pilifera Hook. f. et Thomson	Saxi_pil	18	21	1.43	4833–5084	N,W,S
Iris latistyla Y. T. Zhao	Iris_lat	14	20	1.40	4888–5099	N,W,S
Thymus linearis Benth. ex Benth	Thym_lin	2	5	1.40	4962–5005	S
Rhodiola smithii (Hamet) S. H. Fu	Rhod_smi	6	9	1.33	4888–5104	N,W,S

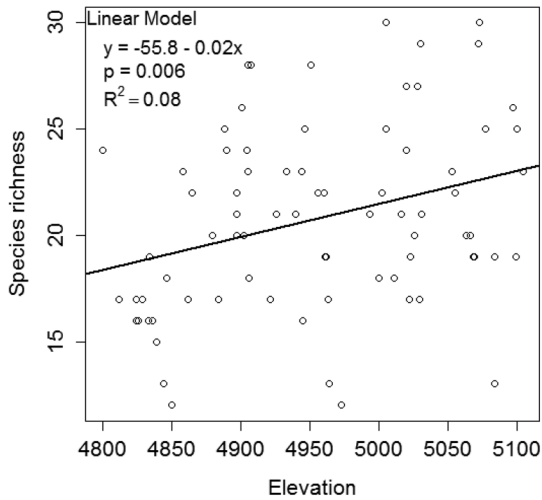| Species	Abbreviation	Plots	Quadrats	Abundance	Elevation	Aspect
Microgynoecium tibeticum Hook.f.	Micrg_tib	3	3	1.33	4839–5099	W,N
Onosma waltonii Duthie	Onos_wal	7	8	1.25	4890–5028	S,N
Cerastium fontanum Baumg. subsp. *triviale* (Link) Jalas	Cera_fon	8	10	1.20	4826–5104	N,W,S
Artemisia wellbyi Hemsl. et Pearson	Art_wel	5	5	1.20	4824–5100	N,W,S
Rhodiola cretinii (Hamet) H. Ohba subsp. *sino-alpina* (Fred) H.Ohba	Rhod_cre	4	6	1.17	5020–5077	N,W,S
Dimorphostemon glandulosus (Kar et Kir) Golubk.	Dimo_gla	3	4	1.00	4901–5100	W,N
Pomatosace filicula Maxim	Poma_fil	3	3	1.00	5028–5084	N,W,S
Astragalus donianus DC	Astr_don	2	2	1.00	5002–5023	N
Astragalus confertus Benth ex Bunge	Astr_con	1	1	1.00	4940	S
Incarvillea younghusbandii Sprague	Inca_you	4	4	1.00	4884–5073	N.S
Trigonotis sp.	Trig_sp.	1	1	1.00	5068	W
Bupleurum candollei Wall. ex DC	Bupl_can	2	2	1.00	4824–4850	W
Anaphalic sp.	Ana_sp.	2	4	1.00	4960–5097	N
Rhodiola bupleuroides (Wall. ex Hook. f. et Thoms.) S. H. Fu	Rhod_bup	1	1	1.00	5073	S
Aconitum sp.	Acon_sp.	1	1	1.00	5055	N
Pegaeophyton minutum Hara	Pega_min	1	1	1.00	5053	W
Pseudostellaria tibetica Ohwi	Pseu_tib	1	1	1.00	5073	S
Corydalis sp	Cory_sp2	1	1	1.00	5073	S
Ranunculus popovii var. *stracheyanus* (Maxim.) W. T. Wang	Ranu_pul	1	1	1.00	5073	S
Microula tibetica Benth	Micrl_tib	2	2	1.00	4946–5073	S

FIGURE A1. Graph illustrating significant relationship between plant species richness (by pooling number of species from five 1 × 1 m quadrats into one plot) and elevation at Nam Tso, Tibet Autonomous Region of China, in 2009. Regression lines were based on estimates of parameters in the linear model.
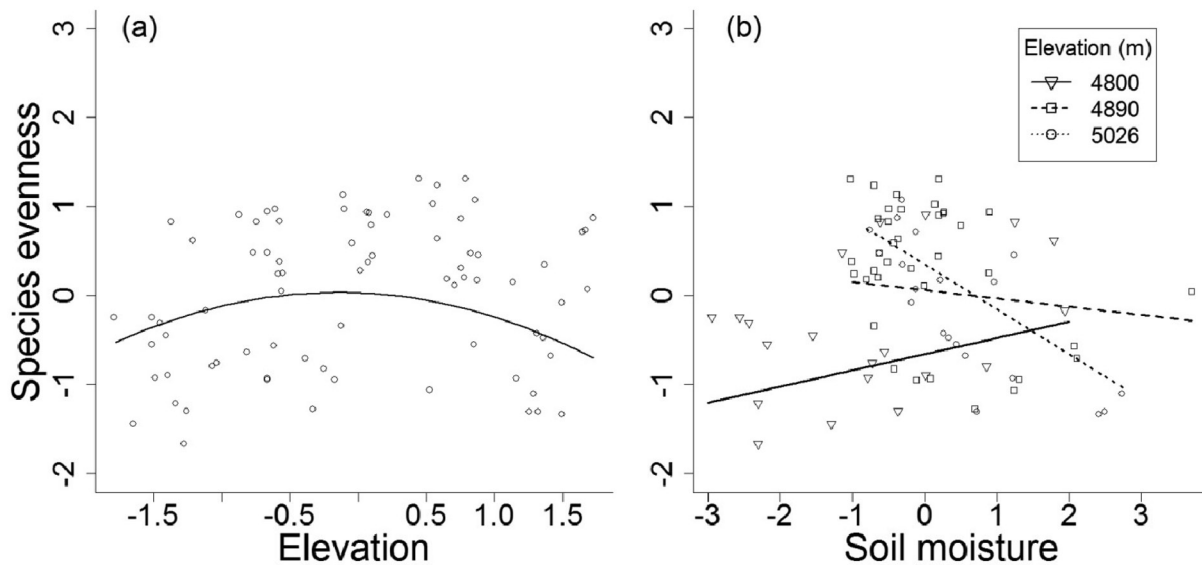

FIGURE A2. Graphs illustrating significant quadratic and interaction terms involved in best subset generalized linear model (GLM) for species evenness (combining data from five quadrats of 1 m² within each combination of elevation and aspect zone in our study area) at Nam Tso, Tibet Autonomous Region of China, in 2009. Regression lines were based on estimates of parameters in the GLM. The explanatory variables used in the full model to derive the best subset models include first and second order terms for elevation, soil moisture, grazing intensity, pika burrow, solar radiation index, and surface roughness, and interaction terms between grazing intensity, elevation, and soil moisture.
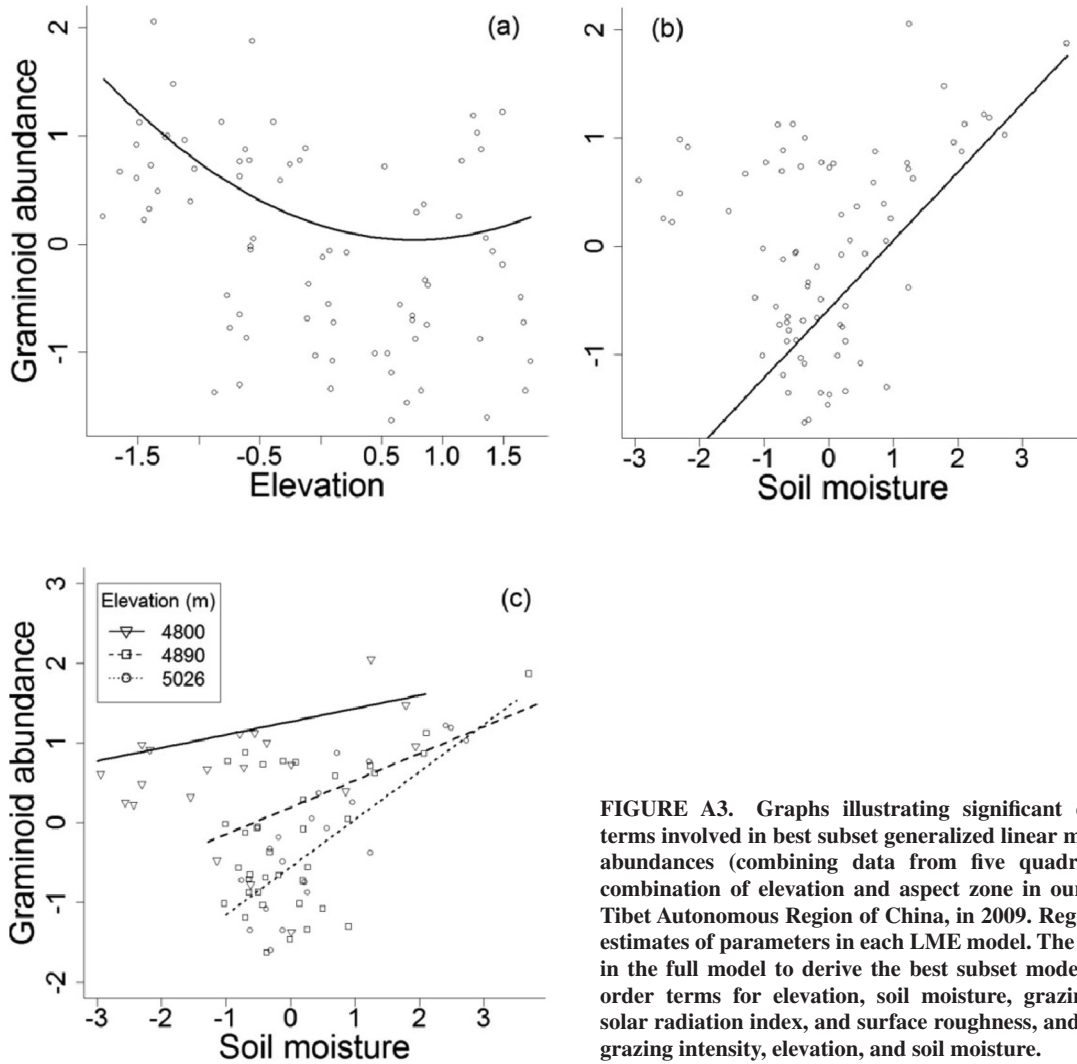
FIGURE A3.   Graphs illustrating significant quadratic and interaction terms involved in best subset generalized linear model (GLM) for graminoid abundances (combining data from five quadrats of 1 m² within each combination of elevation and aspect zone in our study area) at Nam Tso, Tibet Autonomous Region of China, in 2009. Regression lines were based on estimates of parameters in each LME model. The explanatory variables used in the full model to derive the best subset models include first and second order terms for elevation, soil moisture, grazing intensity, pika burrow, solar radiation index, and surface roughness, and interaction terms between grazing intensity, elevation, and soil moisture.
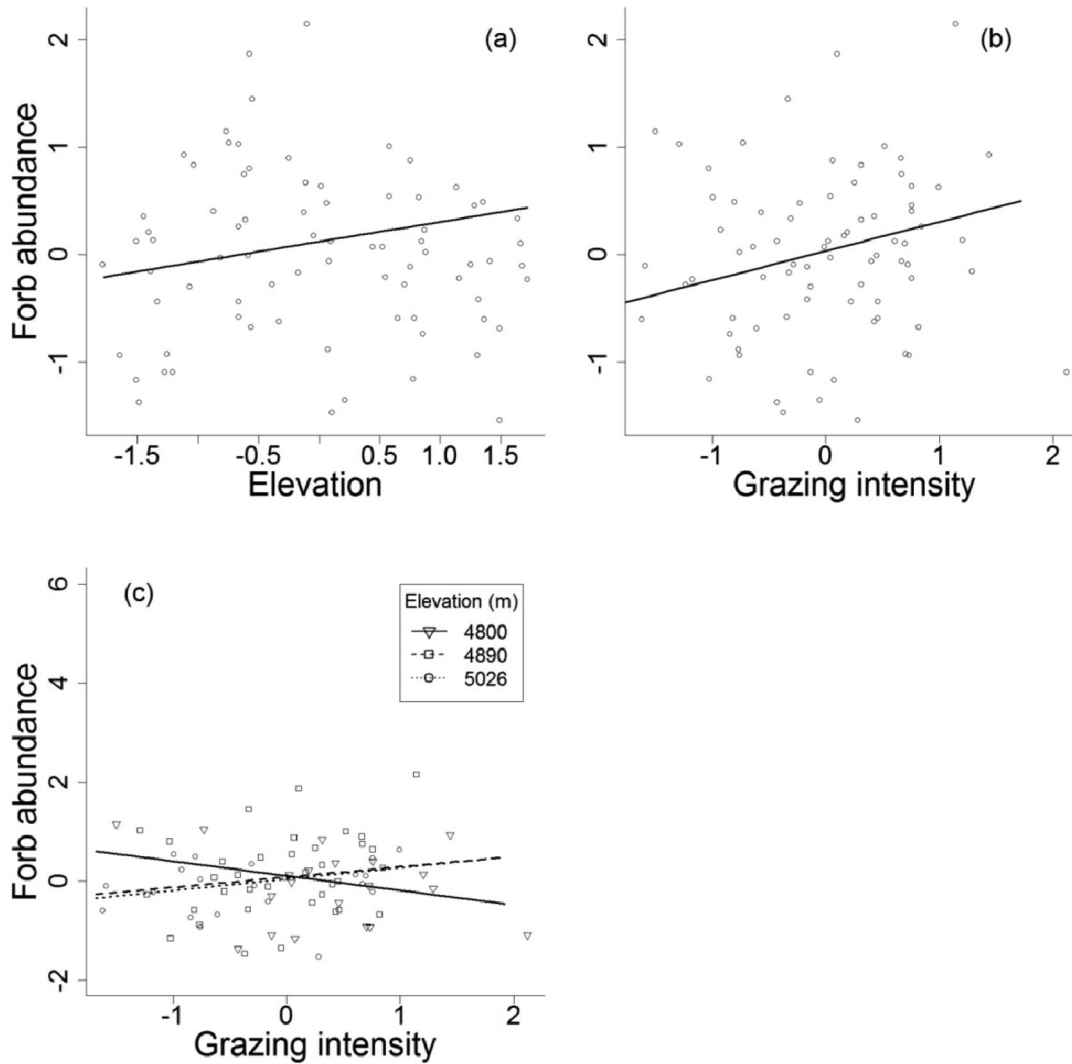
FIGURE A4. Graphs illustrating significant quadratic and interaction terms involved in best subset generalized linear model (GLM) for forb abundances (combining data from five quadrats of 1 m² within each combination of elevation and aspect zone in our study area) at Nam Tso, Tibet Autonomous Region of China, in 2009. Regression lines were based on estimates of parameters in each LME model. The explanatory variables used in the full model to derive the best subset models include first and second order terms for elevation, soil moisture, grazing intensity, pika burrow, solar radiation index, and surface roughness, and interaction terms between grazing intensity, elevation, and soil moisture.
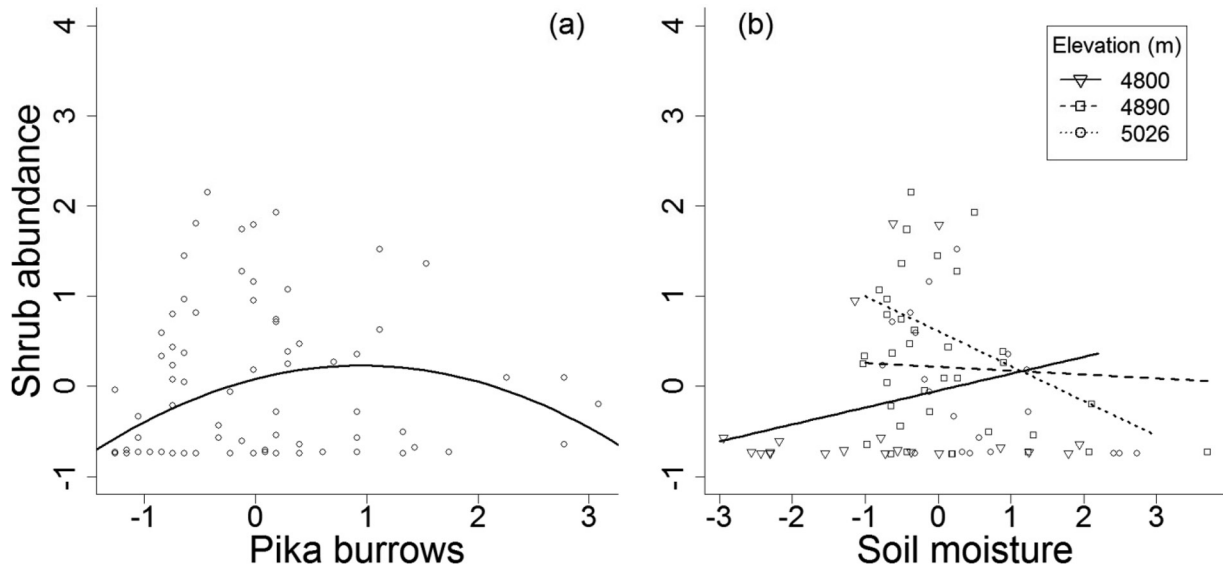
FIGURE A5. Graphs illustrating significant quadratic and interaction terms involved in best subset generalized linear model (GLM) for shrub abundances (combining data from five quadrats of 1 m² within each combination of elevation and aspect zone in our study area) at Nam Tso, Tibet Autonomous Region of China, in 2009. Regression lines were based on estimates of parameters in each LME model. The explanatory variables used in the full model to derive the best subset models include first and second order terms for elevation, soil moisture, grazing intensity, pika burrow, solar radiation index, and surface roughness, and interaction terms between grazing intensity, elevation, and soil moisture.
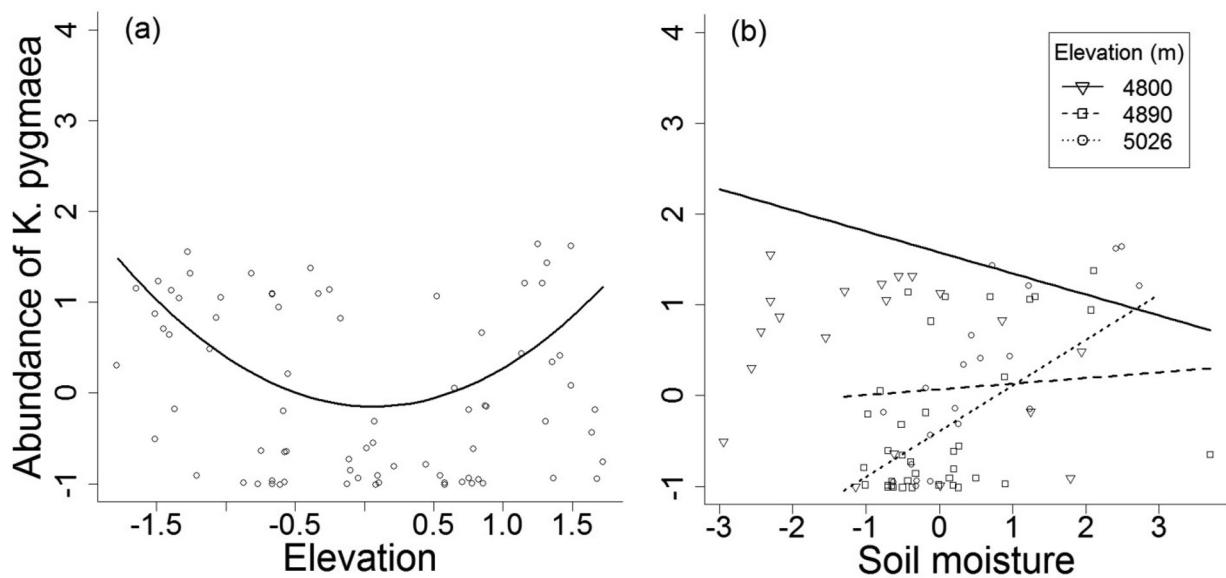

FIGURE A6. Graphs illustrating significant quadratic and interaction terms involved in best subset generalized linear model (GLM) for abundances of Kobresia pygmaea C. B. Clarke (combining data from five quadrats of 1 m² within each combination of elevation and aspect zone in our study area) at Nam Tso, Tibet Autonomous Region of China, in 2009. Regression lines were based on estimates of parameters in each LME model. The explanatory variables used in the full model to derive the best subset models include first and second order terms for elevation, soil moisture, grazing intensity, pika burrow, solar radiation index, and surface roughness, and interaction terms between grazing intensity, elevation, and soil moisture.
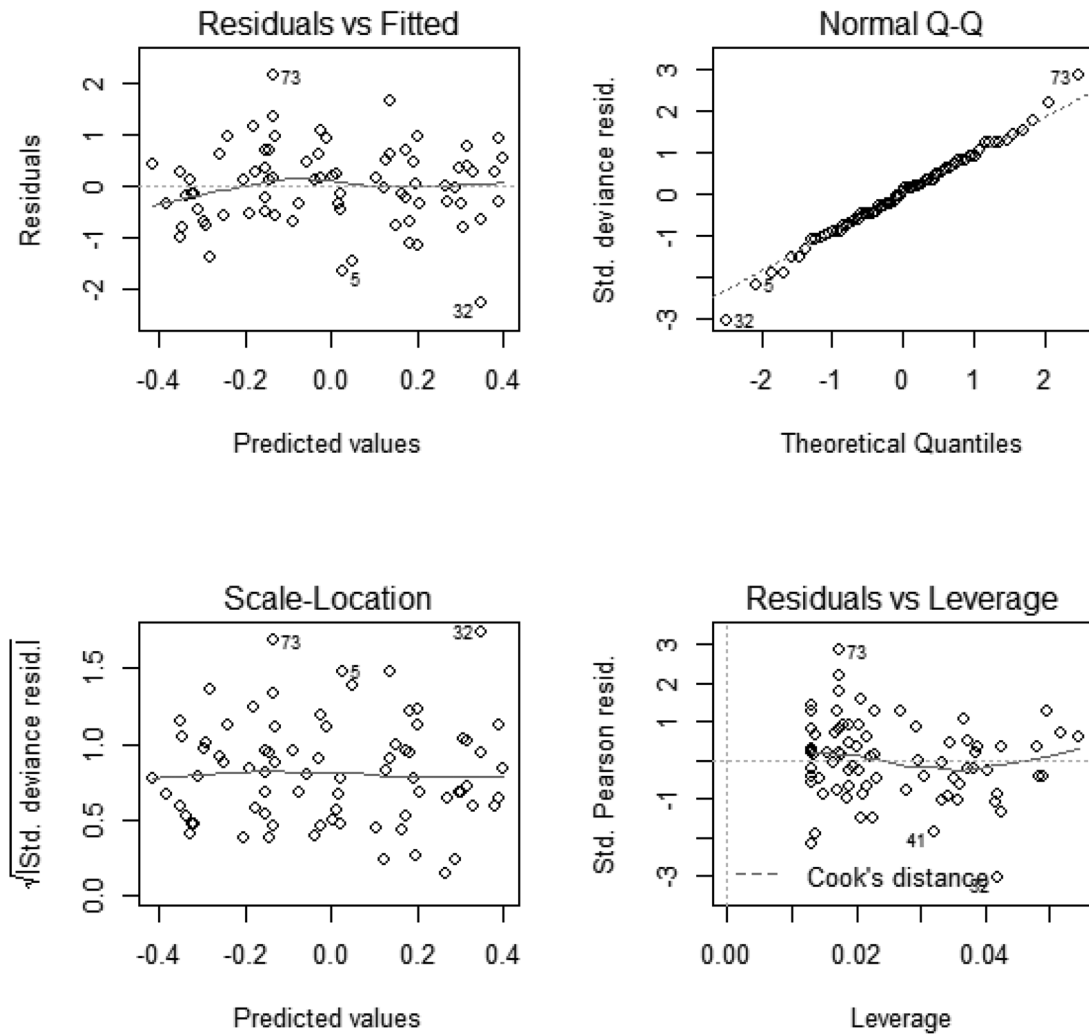
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FIGURE A7. Residual plots for a linear mixed effect model (LME) (response variable: species richness; predictor variables: elevation and quadratic term of soil moisture) to illustrate how we have inspected the model adequacy in the analyses.