

## Predicting plant traits and functional types response to grazing in an alpine shrub meadow on the Qinghai-Tibet Plateau

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The identification of easily measured plant functional types (PFTs) that consistently predict grazing response would be a major advance. The responses to grazing of individual traits and PFTs were analyzed along a grazing gradient in an alpine shrub meadow on the Qinghai-Tibet Plateau, China. Three response types were identified; grazing increaser (GI), grazing decreaser (GD), and neutral (NE) for both traits and PFTs. Seven traits were measured: plant height, economic group, cotyledon type, plant inclination, growth form, life cycle, and vegetative structure. The first five were significantly affected by grazing. Ordinal regressions for grazing response of the seven traits showed that the best single predictors of response were growth form (including the attributes "Scattered", "Bunched" or "Closely Bunched"), and plant inclination ("Rosette", "Prostrate", or "Erect"), followed by economic group ("Shrub", "Grass", "Sedge", "Legume", "Forb", or "Harmful") and plant height ("Tall", "Medium", or "Small"). Within the four optimal traits, the summed dominance ratio (SDR) of small plants, forbs, rosette and bunched plants, invariably increased, while that of tall plants, shrubs, grasses, and erect plants decreased, when grazing pressure was enhanced. Canonical correspondence analysis (CCA) identified eleven explanatory PFTs based on 195 defined PFTs, by combining the different attributes of the four optimal traits. Among explanatory PFTs, the most valuable in predicting the community response to grazing were Tall×Shrub×Erect×Scattered and Small×Forb×Rosette, as these have the closest connections with grazing disturbance and include fewer species. Species richness, diversity, and community evenness, did not differ among grazing treatments because turnover occurred in component species and their relative abundances along the grazing gradient. We have demonstrated that a minimum set of PFTs resulting from optimal individual traits can provide consistent prediction of community responses to grazing in this region. This approach provides a more accurate indicator of change within a changing environment than do univariate measures of species diversity. We hope to provide a link between management practices and vegetation structure, forming a basis for future, large scale, plant trait comparisons.

### Alpine shrub meadow, grazing response, optimal traits, plant functional types

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Land use and management practices induce responses and consequent changes within plant communities. The prediction of plant community responses to human factors is therefore a major objective in both applied and theoretical

ecology. Plant responses are usually observed at population or species levels. However, results from studies of particular communities cannot be generalized beyond local situations. Community responses observed in floristically distinct regions require comparison, integration, and extrapolation to enable prediction in new situations [1]. There is thus a growing need to understand plant responses to land man-

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agement factors in terms of plant traits that are easily measured and also ecologically meaningful [2–4].

The concept of plant functional type (PFT) proposes that species can be grouped according to common responses to the environment and/or common roles within ecosystems [5, 6]. The PFT framework is able to reduce the complexity of species diversity to a few key plant types [7]. It constitutes a useful tool for predicting changes in vegetation and biodiversity as consequences of environmental disturbance and land use changes, at regional and global scales [8]. It is not only helpful for understanding the mechanisms behind changes in vegetation, but also for predicting these changes [9]. However, the crucial problem in using the PFT framework is how to define plant types. Because types are described by traits, the problem has been translated into how to select the most optimal traits. PFTs can be defined as combinations of traits, and the best traits are those that optimize association between vegetation type and environmental variation [10]. These traits reflect ecological responses to nutrient input and/or defoliation frequency. If environmental change causes species change, then this will result in modified ecosystem function via change in representation of these traits [11].

Grazing disturbance by domestic herbivores has both extensive and profound impacts on grassland. The identification of PFTs that explain and predict the responses of plant species and communities to grazing is a key tool in the management of grazing systems [1], and in identifying species that are vulnerable to land use changes at a local scale [12]. There is presently an ongoing international effort to identify PFTs or a minimum set of the most important plant traits that must be considered in relation to grazing response, for the purposes of predicting vegetation dynamics [1, 8, 13–18]. Almost a century of empirical research into rangelands in different parts of the world has been dedicated to identifying the responses of individual species to varying grazing intensities. This has led to the formulation of generalizations about plant types and traits associated with negative and positive responses to grazing, i.e. plants decreased in abundance by grazing or those that are able to increase and invade [1, 13, 19]. Recent analyses of the significance of selected traits have considered mostly “soft” traits because these are morphological or behavioral, and are easily measured across a large number of species and sites [17]. Chosen traits thus need to be easy to recognize in the field, and useful to rangeland managers. A meta-analysis of plant trait responses to grazing, based on 197 studies covering all major regions of the world, demonstrated that species responses to grazing closely correlate with morphological characters [20]. McIntyre et al. [21] also stressed the importance of identifying trait attributes that are linked with specific disturbance regimes, and attributes that are functionally significant in a specific ecosystem. However, which morphological traits are most valuable and what are the best

PFTs for predicting responses to grazing in any given area, remain shrouded by controversy [1, 15, 17–19, 22–24]. Subsequently, several studies investigating the relationship between functional traits and species abundance, in response to grazing in different ecosystems, have produced inconsistent conclusions [12, 18, 20, 24–29]. Whether simple, measurable, functional traits can predict changes in species abundance in response to grazing remains unclear.

We carried out an experiment to evaluate the responses of measured plant traits and PFTs to long-term grazing in an alpine shrub meadow, at the Haibei Research Station on the north-eastern Qinghai-Tibet Plateau, China. The Qinghai Tibet Plateau is highly vulnerable to ongoing climatic and land use changes [30]. Over the last fifty years, most of the area has been grazed by Tibetan sheep and yaks at moderate to heavy intensities. Grazing is the main factor affecting ecosystem degradation through long-term change including vegetation loss. Overgrazing, in particular, has led to severe degradation of 30% of the alpine meadow [31, 32], and is probably the most important factor causing grassland degradation [31]. Under intensive grazing in the alpine shrub meadow at the Haibei Research Station, for example, dominant shrubs and accompanying tall, perennial, bunch-grasses disappeared, and were partly replaced by some typical forbs. In this way the monodominant community became a polydominant community only 20 years [33]. The aboveground biomass of shrubs, grasses, sedges and litter decreased, and that of low quality forbs increased, as grazing density increased [31, 33–35]. As a result, the index of grassland quality for the community clearly decreased [35]. To investigate the utility of PFTs as indicators of long-term vegetation change in response to grazing in alpine shrubland ecosystems, we performed a functional type analysis based on predictive statistical modeling. Using a proportional odds model [36], we first identified optimal traits in response to grazing, to find the most valuable ‘soft’ traits for predicting species response. Second, because different PFTs will respond differently to grazing, and PFT diversity may be related to ecosystem stability [5, 17], we proposed that fluctuations in grazing intensity have selected for different PFTs and should result in turnover of PFTs along grazing gradients. If so, the PFTs that show lowest variability when faced with grazing disturbance are the most important in determining community and/or ecosystem stability. Conversely, those showing the largest variability are the most valuable in predicting community dynamics. Finally, using canonical correspondence analysis (CCA) [37], we estimated the relative contributions of our PFTs to vegetation dynamics. Our aim was to answer the following questions: (1) Which “soft” traits can explain and predict grazing response within alpine shrub meadows? (2) Which PFTs are most important in determining community and/or ecosystem dynamics? (3) What is the ecological significance of the functional response of the community?

## 1 Materials and methods

### 1.1 Site description

The research was conducted at the Haibei Research Station (37°29'N, 101°12'E, 3100 m elevation) in the province of Qinghai, China, situated in the northeast of the Qinghai-Tibet Plateau, in a broad NW-SE oriented valley, and surrounded by the Qilian Mountains. Mean annual precipitation is 562 mm, over 80% of which falls as rain during the summer growing season between May and September. Mean annual air temperature at the site is -1.6°C; mean air temperature during the warmest month (July) is 18°C. Fenced experimental grazing pasture was situated in *Potentilla fruticosa* shrubland (3300–3400 m elevation), which is usually a cooler, summer-autumn grazed pasture at an elevation of 3150–3800 m [31, 38–40]. It was reported that there were about 45 species (including 3 shrubs, 1 half-shrub, and 41 herbs) from 16 families and 36 genera [41]. The dominant species is *Potentilla fruticosa*, and companions are *Kobresia capillifolia*, *Festuca rubra*, *Stipa penicillata* and *Potentilla nivea*. Community cover is about 60%–93% [33, 38]. The main plant life-forms are hemicryptophytes (62.22%), geophytes (28.89%), and phanerophytes (8.89%) [41]. Net aboveground production varies from 176.1–266.72 g m<sup>-2</sup> a<sup>-1</sup> [31, 41]. Biomass percentages of forbs, grasses, shrubs, sedges and litter are about 30.16%, 24.03%, 23.95%, 14.75% and 7.11%, respectively [41]. The soil type is alpine shrub meadow soil [38]. The dominant shrub species, *P. fruticosa*, grows about 40–50 cm high. The main dominant herbs, *Stipa aliena*, *Elymus nutans*, *Ptilagrostis dichotoma*, and *Kobresia capillifolia*, are about 20–40 cm in height. The main accompanying herbs, *K. humilis*, *Saussurea superba*, *Potentilla nivea*, *Oxytropis glaba*, *Pedicularis oederi* var. *sinensis*, *Gentiana straminea*, *G. farreri*, and *Leontopodium longifolium*, are about 5–15 cm in height [39].

### 1.2 Grazing experiments

The experimental grazing pasture (5.97 ha) was established in 1985 [31, 39, 41]. The fence was about 1.20 m high, comprised of seven strands of barbed wire fixed to angle-iron posts. Randomized complete block design was used for the experiment, involving three replicates and four levels of grazing intensity. Grazing was conducted by healthy, two year old, Tibetan wethers. Average live-weight per wether was about 20 kg. Different sheep with similar weight were used each year. Between 1985 and 1997, grazing intensities (number of Tibetan sheep/ha) at each of the four levels were: about 0.00 (ungrazed control, UG; block area = 0.30 ha), 2.55 (light grazing, LG; block area = 0.31 ha), 4.30 (moderate grazing, MG; block area = 0.47 ha), and 5.35 (heavy grazing, HG; block area = 0.91 ha) [31, 33–35, 39–41]. Between 1998 and 2001, grazing intensity of three

of the treatments changed to about 2.00, 4.00, and 8.00 [42]. Grazing lasted from the first week of June to the last week of October, in all years, and was consistent with the period of free-grazing by local farm animals in their summer–autumn pastures. The herbage utilization ratio by experimental animals was about 25%–30%, 40%–45%, and 60%–70% for LG, MG, and HG treatment during the grazing period, for every year since 1985 [31, 33–35, 39–42].

### 1.3 Sampling

Thirty-six quadrats (4 grazing levels × 3 blocks × 3 quadrats per block; quadrats 1 m × 1 m in size) were randomly located in the experimental pasture in early spring of 2001. Each of the quadrats was covered with a cube-shaped wire frame (1.5 m × 1.5 m × 0.7 m) to prevent the sheep defoliation until the sampling date, in order to reveal the effects of long-term grazing on the plant community. Data from all herbaceous species were collected from these quadrats during August 5–10, 2001. Plant height (the highest stem), plant density, and coverage of each herbaceous species, were measured using the point method [30]. In addition, we similarly located thirty-six large quadrats (5 m × 5 m) to collect data relating to three shrub species, *Potentilla fruticosa*, *Spiraea alpina* and *Salix oritrepha*. Their canopy height, plant density (area conversion was performed from 25 m<sup>2</sup> to 1 m<sup>2</sup> following measurement), and canopy coverage, were measured using the ratio of canopy area (minor axis length multiplied by prolate axis length of canopy) to large quadrat area. These data were used to compute species richness (SR), the summed dominance ratio (equal to relative density plus relative coverage, SDR) of each species and the Shannon-Wiener ( $H'$ ) diversity index of each quadrat. To facilitate interpretation of  $H'$ , we took the antilog of the Shannon index ( $e^{H'}$ ); this is the number of species that would, if each was equally common, produce the same  $H'$  as the sample [30].

### 1.4 Classification of PFTs

To investigate in some detail the response of PFTs to grazing, we initially divided the 69 encountered species into 21 trait attributes using seven candidate traits. Following our field observations and published literature the seven chosen traits were: plant height (tall plants, >40 cm; medium plants, 20–40 cm; small plants, <20 cm), economic group (Shrub, Grass, Sedge, Legume, Forb, or Harmful (spiny or toxic)), cotyledon type (Monocotyledon or Dicotyledon), life cycle (Perennial or Annual), plant inclination (Rosette, Prostrate, or Erect), growth form (Scattered, Bunched, or Closely Bunched), vegetative structure (Rhizomatous, Stoloniferous, or Climbing) [1, 13, 19, 39, 41, 43–45]. Information about categorical traits was also compiled from the literature, including the *Flora of Tibet* and *Iconographia Cormophytorum Sinicorum*. Because a unique PFT is likely to include

one or several unique traits, we chose to define a PFT as the sum of all possible combinations of different trait attributes. Pillar [10] similarly considered combinations of trait attributes to optimize the perception of association between vegetation dynamics and grazing disturbance. By assembling all possible attributes of each candidate trait, we obtained different kinds of PFT, and termed these one-trait PFTs, two-trait PFTs, three-trait PFTs, and four-trait PFTs.

### 1.5 Data analysis

Differences in species richness (SR), species diversity ( $H'$ ), and species evenness (E) among treatments were analyzed using ANOVA (SPSS 13.0 for Windows, SPSS Inc.). Tukey's post-hoc tests (SPSS 13.0 for Windows, SPSS Inc.) were carried out to test differences among means. Many authors have classified plant response types to grazing using the categories "grazing increasers" (GI), "neutral" (NE), or "grazing decreaseers" (GD) from the species abundances in sites with contrasting grazing intensities [1, 13, 19, 26]. Some studies have distinguished monotonic from non-linear, unimodal responses to grazing intensity [1, 13, 19, 46–48]. Our approach was to search the species-traits-grazing disturbance space for a minimum set of functional traits able to generate the best predictions of PFTs along a grazing disturbance gradient. We focused on predictive statistical modeling and direct gradient analysis. First, we conducted curve regressions using the curve estimation method (SPSS 13.0 for Windows, SPSS Inc.) for SDR ( $Y$ ) at grazing intensity ( $X$ ), to determine the grazing response type of a single species or of a trait attribute. Three basic response shapes were expected: GI, GD, and NE (i.e. curve regressive models were not significant,  $P > 0.05$ ). These statistical models were selected to maximize  $R^2$ . Data  $\ln(x+1)$  transformations were considered for these regression models. Second, we defined the grazing response as dependent variables to be predicted, and seven candidate traits as independent variables or potential predictors. Because grazing response is a multistate categorical variable, we used an ordinal logistic regression model [36]. Analyses using seven candidate traits were then carried out in search of the 'best traits' model for prediction of grazing response, i.e. the model with the highest parameter estimate. Model and predictor significance were obtained using the Wald test statistic (SPSS 13.0 for Windows, SPSS Inc.), assuming a chi-square distribution with 1 *df*. Based on this we were able to choose an optimal subset from the initial trait set.

Finally, we employed canonical correspondence analysis (CCA) through CANOCO for Windows software [37], to determine the optimal PFT subset for predicting vegetation dynamics. CCA can estimate the proportion of variance in the response data that is accounted for by the explanatory variables, allow the comparisons of the effects of explanatory variables on response variables, and then lead researchers to exclude uninformative or redundant explanato-

ry variables from future analyses [49]. We ran CCA separately for one-trait, two-trait, three-trait, and four-trait PFTs. Summations of the SDRs of PFTs that were similar in response type were defined as response variables GI, GD or NE. These were able to indicate vegetation dynamics. The SDR of each PFT was defined as an explanatory variable. Each quadrat was considered one sample for the purposes of CCA. Because the number of PFTs resulting from different combinations of attributes was likely to be greater than the number of samples, stepwise forward selection was used to choose the subset of optimal PFTs with the greatest explanatory power, from the total PFT set [50]. PFTs with  $p$  values less than 0.05 were derived through Monte Carlo permutation tests, using 499 permutations.

## 2 Results

### 2.1 Plant responses to grazing

No marked differences in SR,  $H'$ , or E, were observed after 16 years of controlled management (Table 1). Species numbers ranged from 29 to 34 across grazing treatments. Of the 69 species encountered, only 12 (i.e. GI plus GD) were significantly different in their SDRs across grazing treatments ( $P \leq 0.05$ ). The GI group comprised four species (5.80%), and the GD group, 8 species (11.6%). The residual 57 species (82.6%) were neutral. However, there were considerably higher proportions of forbs, dicotyledons, perennials, scattered, and those plants without vegetative structures in GI and GD groups (Table 2). Harmful plants were not always more frequent as GI, in fact there was a slight reverse tendency (Table 2). *Morina chinensis*, *Thermopsis lanceolata*, and *Ligularia sagitta*, for example, are often classified as GI because of their dense spines or deterrent chemicals [51, 52]. We found, however, they were GD or NE. Despite the perplexing grazing response of some species, we found a significant association between response and particular traits. These included plant height, plant inclination, and economic group. No "tall" plants, "shrubs" or "grasses" were GI, for example, but "small" plants and "rosette" plants accounted for 75% and 50% of GI. All GD species had erect stems (Table 2).

### 2.2 Best 'soft' trait predictors of response to grazing

Curve regressions showed that the SDRs of medium plants, sedges, legumes, harmful plants, life cycle, and vegetative structure, were nonsignificantly correlated with grazing intensity ( $P > 0.05$ ). The SDRs of small plants, forbs, dicotyledons, rosette and bunched plants, invariably increased, while those of tall plants, shrubs, grasses, monocotyledons, and erect stem plants, invariably decreased with increased grazing pressure (Table 3). An ordinal logistic regression model showed that the chi-square for covariates of  $-2 \log$ -likelihood was 340.1 ( $df = 6$ ,  $P < 0.001$ ) (Table 4). This

**Table 1** ANOVA for species richness (SR), species diversity ( $H'$ ) and evenness index ( $E$ ), of the alpine shrub meadow<sup>a)</sup>

Index	Grazing intensity (Tibetan sheep/ha)				$F_{3,24}$	Significance
	UG	LG	MG	HG		
SR	32.67±1.10	29.67±3.64	32.89±2.26	34.22±3.31	2.041	0.135
$H'$	2.88±0.05	2.81±0.16	2.97±0.09	2.98±0.17	0.963	0.426
$E$	0.59±0.30	0.60±0.06	0.58±0.11	0.58±0.69	0.385	0.765

a) UG=ungrazed control; LG=light grazing; MG=moderate grazing; HG=heavy grazing.

**Table 2** Cross-tabulation of the sixty-nine species by grazing response type, and by seven candidate traits<sup>a)</sup>

Trait	Attributes	Responses types			Total
		GI	GD	NE	
Plant height	Tall	0 (0)	3 (37.5)	9 (15.78)	12 (17.4%)
	Medium	1 (25)	2 (25)	12 (21.05)	15 (21.8%)
	Small	3 (75)	3 (37.5)	36 (63.16)	42 (60.8%)
	Shrubs	0 (0)	1 (12.5)	2 (3.51)	3 (4.4%)
Economic group	Grasses	0 (0)	1 (12.5)	8 (14.04)	9 (13.1%)
	Sedges	0 (0)	0 (0)	5 (8.77)	5 (7.3%)
	Legumes	0 (0)	0 (0)	2 (3.51)	2 (2.9%)
	Forbs	3 (75)	5 (62.5)	26 (45.61)	33 (47.8%)
	Harmful	1 (25)	1 (12.5)	14 (24.56)	17 (24.6%)
Cotyledon type	Monocotyledon	0 (0)	1 (12.5)	15 (26.32)	16 (23.2%)
	Dicotyledon	4 (100)	7 (87.5)	42 (73.68)	53 (76.8%)
Life cycle	Perennial	4 (100)	7 (87.5)	50 (87.72)	61 (88.4%)
	Annual	0 (0)	1 (12.5)	7 (12.28)	8 (11.6%)
Plant inclination	Erect	1 (25)	8 (100)	33 (57.89)	42 (60.9%)
	Prostrate	1 (25)	0 (0)	16 (28.07)	17 (24.6%)
	Rosette	2 (50)	0 (0)	8 (14.04)	10 (14.5%)
Growth form	Closely Bunched	0 (0)	2 (25)	17 (29.82)	19 (27.5%)
	Bunched	1 (25)	1 (12.5)	12 (21.05)	14 (20.3%)
	Scattered	3 (75)	5 (62.5)	28 (49.12)	36 (52.2%)
Vegetative structure	Absent	3 (75)	5 (62.5)	43 (75.44)	51 (74.0%)
	Present	1 (25)	3 (37.5)	14 (24.56)	18 (26.0%)
Total		4 (5.8%)	8 (11.6%)	57 (82.6%)	69 (100%)

a) All recorded species were divided into twenty-one attributes according to plant height, economic group, cotyledon type, life cycle, plant inclination, growth form, and vegetative structure. Grazing response type of a species was determined by curve regressions using the curve estimation method for the SDRs of each species ( $Y$ ) at grazing intensity ( $X$ ). Three types of grazing response were found: GI = grazing increaser; GD = grazing decreaser; NE = neutral. Numbers (and percentages of column totals) indicate numbers of species in a particular grazing response type within each trait attribute.

**Table 3** Grazing responses of different trait attributes were measured by the curve estimation method for the SDRs of the attributes of each trait ( $Y$ ), to grazing intensity ( $X$ )<sup>a)</sup>

Traits	Attributes	Curve estimation	
		Response models of trait' SDR to grazing	Response types
Plant height	Tall	$Y=2.96-0.13X, R^2=0.18, F_{1,34}=7.350, P=0.010$	GD
	Medium	ns	NE
	Small	$Y=3.92+0.05X, R^2=0.31, F_{1,34}=15.43, P=0.000$	GI
	Shrubs	$Y=2.45-0.13X, R^2=0.14, F_{1,34}=5.29, P=0.028$	GD
Economic group	Grasses	$Y=2.84-0.07X, R^2=0.22, F_{1,34}=9.47, P=0.004$	GD
	Sedges	ns	NE
	Legumes	ns	NE
	Forbs	$Y=3.84-0.05X, R^2=0.27, F_{1,34}=12.76, P=0.001$	GI
	Harmful	ns	NE
Cotyledon type	Monocotyledon	$Y=3.14-0.03\ln X, R^2=0.15, F_{1,34}=5.96, P=0.020$	GD
	Dicotyledon	$Y=4.36+0.01\ln X, R^2=0.17, F_{1,34}=7.12, P=0.012$	GI
Life cycle	Perennial	ns	NE
	Annual	ns	NE
Plant inclination	Erect	$Y=4.11-0.04X, R^2=0.19, F_{1,34}=8.16, P=0.007$	GD
	Prostrate	ns	NE
	Rosette	$Y=3.23+0.06X, R^2=0.17, F_{1,34}=6.84, P=0.013$	GI
Growth form	Closely Bunched	ns	NE
	Bunch	$Y=2.55+0.12X, R^2=0.26, F_{1,34}=11.84, P=0.002$	GI
	Scattered	ns	NE
Vegetative structure	Absent	ns	NE
	Present	ns	NE

a) ns: No significant difference at  $p=0.05$ . All recorded species were divided into twenty-one attributes according to plant height, economic group, cotyledon type, life cycle, plant inclination, growth form, and vegetative structure. Three types of grazing responses were found: GI = grazing increaser; GD = grazing decreaser; NE = neutral.

**Table 4** Ordinal regressions for grazing response in terms of the SDRs of traits, with grazing responses as dependent variables, and traits as independent variables

Independent variables	Analysis of maximum likelihood estimates				
	Estimate $\beta$	Wald	df	Sig.	Odds Ratio
Growth form	2.73	51.94	1	0.000	15.33
Plant inclination	2.07	31.21	1	0.000	7.92
Economic group	1.70	21.76	1	0.000	5.47
Plant height	0.97	6.76	1	0.009	2.64
Vegetative structure	$1.33 \times 10^{-8}$	–	1	1.000	1.00
Life cycle	$1.33 \times 10^{-8}$	–	1	1.000	1.00
Cotyledon type	0 <sup>a</sup>	–	0	–	–

a) This parameter is set to zero because it is redundant. Grazing response types were determined according to the results in Table 2.

model was statistically significant. The Wald test showed that independent variables such as growth form, plant inclination, economic group, and plant height, significantly contributed to the predictive model. The order of odds ratio (the absolute value of  $e^{\beta}$ ) was growth form > plant inclination > economic group > plant height. This indicated that the greatest single trait response was obtained when all 69 species were categorized according to growth form or plant inclination. The second and third best predictors of trait response were economic group and plant height. Life cycle, vegetative structure, and cotyledon type, had lower odds ratio values or were not significant predictors of grazing response (Table 3). Thus, the selected four traits (growth form, plant inclination, economic group, and plant height), were treated as an optimal trait set for the prediction of community response. The other traits were eliminated from the following analysis. It is clear that the estimation power of different attributes differs even within an optimal trait. Appendix 1 lists the plant species involved in optimal trait attributes.

### 2.3 Best PFT predictors of response to grazing

We defined a total of 195 PFTs, of four kinds (one-trait, two-trait, three-trait, and four-trait) by assembling all possible attributes of the four optimal traits discussed above (Table 5). The numbers of four kinds of PFTs was 21, 61, 82, and 31, respectively. Response types GI and GD were clearly lower than response type NE across all the PFTs (Table 5). All of the defined 195 PFTs and their response models are shown in Appendix 2.

Our CCA model showed that the effects of explanatory variables (i.e. different PFTs) are highly significant ( $P = 0.002$  or  $P = 0.004$  with 499 permutations). Of the 195 available PFTs, forward selection and a Monte Carlo permutation test allowed eleven explanatory PFTs, as the optimal PFTs subset. The numbers of four kinds of PFTs involved in the optimal PFTs subset was 1, 2, 4 and 4, respec-

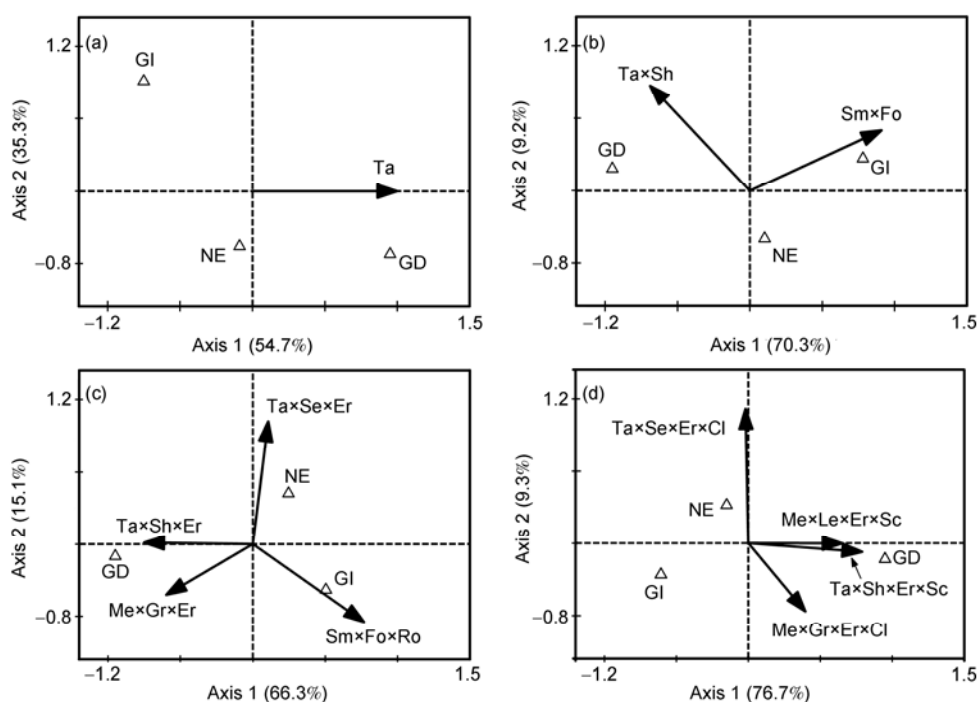
**Table 5** PFTs corresponding to optimal traits were determined according to the order of absolute values of the odds ratio (Table 4) and the grazing response model of the SDR of each PFT<sup>a)</sup>

PFTs	No. of PFTs	Response types	Amount	Proportion (%)	No. of explanatory PFTs
One-trait PFTs	21	GI	5	23.8	0
		GD	5	23.8	1
		NE	11	52.4	0
Two-trait PFTs	61	GI	12	19.7	1
		GD	15	24.6	1
		NE	34	55.7	0
Three-trait PFTs	82	GI	17	20.7	1
		GD	13	15.9	2
		NE	52	63.4	1
Four-trait PFTs	31	GI	6	19.4	0
		GD	3	9.7	3
		NE	22	70.9	1

a) PFTs were defined by four optimal traits and fifteen attributes, including mature plant height (tall, medium, small), plant inclination (erect, prostrate, rosette), growth form (closely bunched, bunched, scattered) and economic group (Shrub, Grass, Sedge, Legume, Forb and Harmful). Grazing responses of PFTs were measured by the curve estimation method for the SDRs of the PFTs ( $Y$ ), to grazing intensity ( $X$ ). Three types of grazing response were found: GI = grazing increaser; GD = grazing decreaser; NE = neutral.

tively (Table 5). Similar patterns of specialization were detected in four graphs (Figure 1). Our CCA ordination diagrams show a clear trend in the distribution of PFTs from the GD end of axis 1 dominated by the PFTs Tall, Tall×Shrub, Tall×Shrub×Erect, Medium×Grass×Erect, Tall×Shrub×Erect×Scattered, Medium×Legume×Erect×Scattered, and Medium×Grass×Erect×Closely Bunched, to the GI end of axis 1 dominated by the PFTs Small×Forb and Small×Forb×Rosette. PFTs Tall×Sedge×Erect and Tall×Sedge×Erect×Closely Bunched were intermediate (NE) (Figure 1). Thus, axis 1 appears to represent a SDR response gradient across the grazing treatments; accounting for 54.7%–76.7% of the total variance, and was correlated mainly with grazing intensity. Axis 2 explained 9.2%–35.3% of the total variance. Effective explanatory PFTs on axis 2 were Tall×Shrub, Small×Forb, Tall×Sedge×Erect, Small×Forb×Rosette, Tall×Sedge×Erect×Closely Bunched, and Medium×Grass×Erect×Closely Bunched (Table 6; Figure 1). The remaining variation in grazing response could not be significantly explained with the available set of explanatory PFTs.

For the one-trait PFTs, PFT Tall was the only significant explanatory variable, and this completely overlapped with axis 1 ( $R_{Ta} = 1.000$ ), revealing that the first two axes accounted for 54.7% and 35.3% of the variance (Table 6; Figure 1(a)). This meant that the other 20 one-trait PFTs (Table 3) did not significantly improve the fit when added to the predictor describing the response to grazing of the community. PFT Tall, however, was a good predictor of grazing response and significantly improved the fit when added to the other one-trait PFTs (Table 6; Figure 1(a)). For the two-trait PFTs, PFT Tall×Shrub and Small×Forb similarly revealed the first two axes, accounting for 70.3% and 9.2% of



**Figure 1** CCA ordination diagram using three response variables: GD, GI, and NE, and explanatory PFTs. PFTs are shown by arrows and labeled with their trait attribute combinations (boldface, first two letters only). The centroids of grazing response types are shown by triangles. GI = grazing increaser; GD = grazing decrease; NE = neutral. Significant explanatory variables are displayed by analyzing (a) one-trait PFTs, (b) two-trait PFTs, (c) three-traits PFTs, and (d) four-traits PFTs.

the variance. Because the SDRs of the two PFTs were negatively correlated, they indicated a different direction in the community response to grazing ( $R_{\text{Ta}\times\text{Sh}} = -0.689$ ;  $R_{\text{Sm}\times\text{Fo}} = 0.910$ ) (Table 6; Figure 1(b)). This meant that they were better predictors for the two-trait PFTs. For the four selected explanatory three-trait PFTs, the first two axes accounted for 66.3% and 15.1% of the variance. Best correlated with the first axis were PFTs Tall×Shrub×Erect ( $R_{\text{Ta}\times\text{Sh}\times\text{Er}} = -0.750$ ), and Small×Forb×Rosette ( $R_{\text{Sm}\times\text{Fo}\times\text{Ro}} = 0.769$ ). Thus, these two PFTs were better predictors for the three-trait PFTs. PFT Tall×Sedge×Erect was mainly correlated with the second axis (i.e. NE;  $R_{\text{Ta}\times\text{Se}\times\text{Er}} = 0.852$ ) (Table 6; Figure 1(c)). For the four selected explanatory four-traits PFTs, the first two axes accounted for 76.7% and 9.3% of the variance. PFTs Tall×Shrub×Erect×Scattered, Medium×Grass×Erect×Closely Bunched, and Medium×Legume×Erect×Scattered were both positively correlated, but the former showed a high degree of fit with axis 1 ( $R_{\text{Ta}\times\text{Sh}\times\text{Er}\times\text{Sc}} = 0.791$ ), and was a better predictor for the four-trait PFTs. The last PFT, Tall×Sedge×Erect×Closely Bunched was mainly correlated with axis 2 (i.e. NE;  $R_{\text{Ta}\times\text{Se}\times\text{Er}\times\text{Cl}} = 0.932$ ) (Table 6; Figure 1(d)).

### 3 Discussion

#### 3.1 Responses of plant species and traits to grazing

We did not find clear variation in species richness, diversity or evenness within this community after long-term grazing

(Table 1). Navarro et al. [53] thought that decrease in or elimination of grazing-sensitive groups of species was compensated for by increased growth of species favored by grazing, thus inducing vegetation changes by means of colonization. Pakeman's research [54] showed that increased grazing intensity was accompanied by an increase in species with a ruderal strategy, rosette habit, higher requirements for light, and lower minimum height. Our previous study on our experimental site showed turnover of component species and their relative abundances along a grazing gradient [42], owing to large differences in resistance to herbivory [17], and in the ability of grazing to shift species composition and relative abundance [19]. We have currently found that as grazing intensity increases, decreases in the SDR of GD (including species or trait attributes) may be approximately compensated for by increases in the SDR of GI. The decrease in grazing-sensitive PFTs subjected to heavy grazing was associated with an increase in grazing-tolerant PFTs, able to use the limited available resources in bare soil patches under heavy grazing conditions. It has been reported that in an alpine meadow area, stocking rates were negatively correlated with organic matter, organic carbon, total nitrogen and total phosphorus in the soil [55, 56]. Fencing, however, was positively correlated with organic matter, total nitrogen, available nitrogen, total phosphorus and available phosphorus [57]. Soil nitrogen availability after heavy grazing was not able to meet the growth demand of grasses and sedges, but met the demand of forbs [58]. Thus,

there was turnover in component species and relative abundance [42], and traits and attributes varied (Tables 2 and 3). Many previous studies have suggested that turnover of differently susceptible PFTs (Figure 1), and differences in environmental factors among treatments [55, 58] in response to long-term herbivory, may together induce species diversity to remain almost constant in communities exposed to different grazing pressures [22, 40, 42, 58, 60, 61]. Species composition, as a result, often changes markedly with grazing intensity, yet the number of species and/or the species diversity shows little response to grazing. This certainly may depend on the relative sizes of the species pools and the different responses of their trait attributes—if species pool sizes are equal, then diversity may remain constant across gradients of grazing intensity. If species pools are unequal in size, then overall species diversity could increase or decrease across grazing intensity gradients. We observed a similar or equal proportion of species or trait attributes that had opposite responses to grazing, and a large number of neutral species and attributes in the assemblage (Tables 2 and 3). Therefore, changes in species or trait attributes along the grazing gradient had great impact on species diversity. These scenarios can also be seen in other research, for example, that of Dong et al. [62] in a *Kobresia parva* alpine meadow, central-east Qinghai-Tibet Plateau, and that of Yi et al. [63] in a true steppe in the Xiling River Basin, Inner Mongolia, China. The results of these studies imply that invariable species diversity along a grazing gradient was very likely to hide turnover in component species or functional traits, following changing grazing pressure. Thus, univariate measures of species diversity are not necessarily good indicators of biodiversity.

We searched for the best predictor set of traits in response to grazing; these were four out of the seven candidate traits: growth form, plant inclination, economic group, and plant height (Table 4). Using the other traits, life cycle, vegetative structure, and cotyledon type, led to models with less predictive value. This indicates a trait response hierarchy [18]; these four traits are superior to the others in determining grazing disturbance. We found that the response directions of these best traits were consistent with those of other investigations at the regional scale [12, 25, 31, 34, 35, 38–40, 64], and also at the global scale [20]. We suggest that the best traits have a stable pattern and strong repeatability of response to grazing and can act as robust predictors of community response. In addition, these traits had important predictive values because they were often correlated with ecosystem function. In some studies [4, 65], growth form was a very important indicator of ecosystem function, clearly expressing links between the trait, plant response and function. Heavy grazing has often been found to greatly reduce the aboveground biomass, palatable herbage height, and total plant community coverage, resulting in dominant shrub and graminoid species being partially replaced by typical forbs (mainly rosette and small species) [31, 33–35,

41]. Plant inclination can be considered a disturbance regeneration trait, and has been relatively well correlated with aboveground primary productivity in grassland [65]. It has been reported that leaf dry matter content greatly differed among grasses, rosette forbs, and upright forbs, in the same community, and was affected by the defoliation regime [6]. Plant height has been considered an indirect characteristic of the ability to compete for light, and an indicator of relative growth rate [1]. Grazing favors short plants, irrespective of climate and grazing history [20]. Thus, the importance of plant height has been highlighted by many authors [1, 12, 17, 19, 20, 24, 25, 64], despite the fact that alpine plants are generally small, and that other studies have found plant height to be of minor importance in predicting grazing response in alpine areas [12]. From a practical point of view, we believe that our chosen four optimal traits are those best adopted by rangeland managers and local ranchers, as they are simple to measure and require little expertise.

The response patterns of species or traits to grazing may be diverse and context-dependent [17, 54, 66]. We observed that the response to grazing of spiny and toxic plants such as *Morina chinensis*, *Thermopsis lanceolata*, and *Ligularia sagitta*, contradicted with the classical precept of range management (Table 2). Certain traits, such as life cycle, or vegetative structure, were weak rather than significant predictors of community dynamics (Table 3). Díaz et al. [1, 20], observed that in subhumid or humid grasslands with a long evolutionary history of grazing, intense grazing typically favored short plants with high regrowth rates, rather than tough, unpalatable plants. de Bello et al. [12], studying an altitudinal and climatic gradient from Mediterranean rangelands to subalpine grasslands in north-eastern Spain, has shown that thorniness was not related to grazing regime, and that short life span as an adaptation to grazing was different at different sites and had no effect in the subalpine area, because short life span is a less successful adaptation under the colder conditions of high altitudes. In dry systems with a long evolutionary history of ungulate herbivory, grazing did not favor annual plants over perennial plants [20]. In calcareous grassland at fourteen sites in Southwest Germany, no significant differences in life cycle were exhibited between five management treatments between 1974 and 1999; most of these species were perennial [25]. The frequent occurrence of rhizomes and stolons in a subalpine location confirmed their importance, but their responses to grazing were shown to be opposite to each other [12, 54]. Predictive power may thus be limited when using these traits.

To generalize beyond specific localities, it is necessary to understand the adaptive significance of simple functional traits and their predictive capacity for plant responses [1, 14, 15, 21]. Our observed trait shifts truly reflected adaptive responses to long-term grazing, because in prior years all plants were available to grazers, and quadrat plants (covered



**Table 6** Forward selection and the Monte Carlo test for optimal PFTs, and correlation coefficients (*R*) between CCA ordination axes and PFTs, and plant species involved in optimal PFTs<sup>a)</sup>

PFTs	Optimal PFTs (Response types): Monte Carlo test <sup>a)</sup>	CCA ordination			Total inertia	Plant species involved in optimal PFTs (Amount)
		Ei; CPV; <i>R</i>	Ax.1	Ax.2		
One-trait PFTs	<b>Ta</b> (GD): <i>P</i> =0.002; <i>F</i> =32.42	Ei	0.001	0.001	0.002	<b>Ta:</b> <i>Helictotrichon tibeticum</i> , <i>Elymus nutans</i> , <i>Spiraea alpine</i> , <i>Deyeuxia flavens</i> , <i>Potentilla fruticosa</i> , <i>Notopterygium forbesii</i> , <i>Salix oritrepha</i> , <i>Gentianopsis paludosa</i> , <i>Ptilagrostis dichotoma</i> , <i>Kobresia capillifolia</i> , <i>Morina chinensis</i> , <i>Ptilagrostis concinna</i> (12)
		CPV	54.700	90.000		
		<i>R</i> <sub>Ta</sub>	1.000***	0.000		
Two-trait PFTs	<b>Ta×Sh</b> (GD): <i>P</i> =0.002; <i>F</i> =50.49 <b>Sm×Fo</b> (GI): <i>P</i> =0.002; <i>F</i> =16.62	Ei	0.002	0.000	0.003	<b>Ta×Sh:</b> <i>Spiraea alpine</i> , <i>Potentilla fruticosa</i> , <i>Salix oritrepha</i> (3) <b>Sm×Fo:</b> <i>Leontopodium nanum</i> , <i>Leontopodium longifolium</i> , <i>Potentilla anserine</i> , <i>Potentilla bifurca</i> , <i>Potentilla discolor</i> , <i>Stellaria media</i> , <i>Geranium pylzowianum</i> , <i>Saxifraga montana</i> , <i>Gentiana aristata</i> , <i>Gentiana squarrosa</i> , <i>Viola bulbosa</i> , <i>Saussurea superba</i> , <i>Ranunculus pulchellus</i> , <i>Galium verum</i> , <i>Taraxacum mongolicum</i> , <i>Rubia cordifolia</i> , <i>Saussurea kokonorensis</i> , <i>Lancea tibetica</i> , <i>Saussurea nigrescens</i> , <i>Ranunculus hirtellus</i> , <i>Parnassia trinervis</i> , <i>Stellaria umbellata</i> , <i>Swertia tetraptera</i> , <i>Galium aparine</i> , <i>Polygonum viviparum</i> L. var. <i>angustum</i> , <i>Gentiana lawrencei</i> var. <i>farreri</i> , <i>Euphrasia pectinata</i> , <i>Torularia humilis</i> (28)
		CPV	70.300	79.500		
		<i>R</i> <sub>Ta×Sh</sub> <i>R</i> <sub>Sm×Fo</sub>	-0.689*** 0.910***	0.724*** 0.415**		
Three-trait PFTs	<b>Ta×Sh×Er</b> (GD): <i>P</i> =0.002; <i>F</i> =8.51 <b>Ta×Sex×Er</b> (NE): <i>P</i> =0.004; <i>F</i> =10.41 <b>MexGr×Er</b> (GD): <i>P</i> =0.002; <i>F</i> =18.15 <b>Sm×Fo×Ro</b> (GI): <i>P</i> =0.002; <i>F</i> =26.25	Ei	0.003	0.001	0.004	<b>Ta×Sh×Er:</b> <i>Spiraea alpine</i> , <i>Potentilla fruticosa</i> , <i>Salix oritrepha</i> (3) <b>Ta×Sex×Er:</b> <i>Kobresia capillifolia</i> (1) <b>MexGr×Er:</b> <i>Koeleria cristata</i> , <i>Festuca ovina</i> , <i>Poa orinosa</i> , <i>Festuca rubra</i> (4) <b>Sm×Fo×Ro:</b> <i>Leontopodium nanum</i> , <i>Leontopodium longifolium</i> , <i>Potentilla anserine</i> , <i>Saussurea superba</i> , <i>Taraxacum mongolicum</i> , <i>Saussurea kokonorensis</i> , <i>Lancea tibetica</i> , <i>Saussurea nigrescens</i> , <i>Gentiana lawrencei</i> var. <i>farreri</i> (9)
		CPV	66.300	81.400		
		<i>R</i> <sub>Ta×Sh×Er</sub> <i>R</i> <sub>Ta×Sex×Er</sub> <i>R</i> <sub>MexGr×Er</sub> <i>R</i> <sub>Sm×Fo×Ro</sub>	-0.750*** 0.106 -0.598*** 0.769***	0.010 0.852*** -0.351 -0.540***		
Four-trait PFTs	<b>Ta×Sh×Er×Sc</b> (GD): <i>P</i> =0.002; <i>F</i> =31.37 <b>Ta×Sex×Er×Cl</b> (NE): <i>P</i> =0.002; <i>F</i> =12.79 <b>MexGr×Er×Cl</b> (GD): <i>P</i> =0.004; <i>F</i> =23.39 <b>MexLex×Er×Sc</b> (GD): <i>P</i> =0.002; <i>F</i> =16.99	Ei	0.010	0.001	0.013	<b>Ta×Sh×Er×Sc:</b> <i>Spiraea alpine</i> , <i>Potentilla fruticosa</i> , <i>Salix oritrepha</i> (3) <b>Ta×Sex×Er×Cl:</b> <i>Kobresia capillifolia</i> (1) <b>MexGr×Er×Cl:</b> <i>Koeleria cristata</i> , <i>Festuca ovina</i> , <i>Poa orinosa</i> , <i>Festuca rubra</i> (4) <b>MexLex×Er×Sc:</b> <i>Thermopsis lanceolata</i> (1)
		CPV	76.700	86.000		
		<i>R</i> <sub>Ta×Sh×Er×Sc</sub> <i>R</i> <sub>Ta×Sex×Er×Cl</sub> <i>R</i> <sub>MexGr×Er×Cl</sub> <i>R</i> <sub>MexLex×Er×Sc</sub>	0.791*** -0.019 0.396* 0.654***	-0.059 0.932*** -0.471*** -0.001		

a) \**P*<0.05; \*\**P*<0.01; \*\*\**P*<0.001. A PFTs was defined as a possible combination of attributes of four optimal traits, following Pillar [10], and using between one and four traits. Four optimal traits (and twenty-one attributes) include mature plant height (**Tall**, **Medium**, **Small**), plant inclination (**Erect**, **Prostrate**, **Rosette**), growth form (**Closely Bunched**, **Bunched**, **Scattered**) and economic group (**Shrub**, **Grass**, **Sedge**, **Legume**, **Forb**, **Harmful**). Combinations of abbreviated boldfaced letters indicate a PFT. Three types of grazing response were found: GI = grazing increaser; GD = grazing decreaser; NE = neutral. Ei = Eigenvalues; CPV = Cumulative percentage variance (%); *R* = Correlation coefficients. Note that some plant species contribute to more than one PFT because they have more than one trait.

with a cube-shaped wire frame in early spring until the sampling date) had not been defoliated by herbivory within the current growing season. Thus, the species and trait responses we observed represented long-term grazing effects, rather than the short-term responses of individuals after damage.

### 3.2 Best PFTs to predict response to grazing based on optimal traits

We found that PFT responses to grazing greatly differed about SDRs, and the community appeared as a mixture of three response types, i.e. GI, GD and NE (Table 5 and Appendix 2). Of the eleven optimal PFTs identified by CCA (based on 195 PFTs from four optimal traits), PFTs Tall, Tall×Shrub, Tall×Shrub×Erect, and Tall×Shrub×Erect×Scattered were GD (Table 3 and Appendix 2). These trait attributes

were very sensitive to an increase in herbage use and showed strong declines in their SDRs when grazing intensity increased (Figure 1). As suggested by Zhou et al. [35], most of the species involved in these PFTs were preferentially selected by herbivores because of high conspicuousness (i.e. high plant height and erect stems), and palatability. In contrast, the SDRs of PFTs Small×Forb and Small×Forb×Rosette increased markedly under heavy grazing, and showed some grazing avoidance characteristics because of low conspicuousness (i.e. a short plant height and rosette form), and lack of palatability [35]. Our observed attributes and PFT responses to grazing along the grazing gradient (Tables 3, 6; Figure 1), can be explained best by the opening of establishment gaps in the closed sward (from none to moderate intensity), and by the vertical differential defoliation gradient imposed by herbivores (at moderate to heavy grazing). This process becomes the major mechanism of

grassland change [19]. Our results suggested a turnover in PFT composition with different responses along a grazing gradient; similar to the response pattern of species. Moreover, either the number of species or PFTs belonging to response type NE was much greater than those of the other two types (Tables 2 and 5). These neutral PFTs and/or species may have served as a useful buffer against grazing pressure, and may be important in maintaining long-term community stability. It has been reported that long-term, heavy grazing simplified the structure of an alpine shrub community, but that the variability in the ecosystem's net primary production was lower than annual precipitation and annual mean air temperature over 40 years [59]. This was despite the aboveground biomasses of shrubs and grasses decreasing and the biomass of forbs increasing, as grazing intensity increased [31]. We believe that the relative stability of net primary production is directly connected with the presence of these neutral PFTs and/or neutral species. Provided that the trait attributes of these neutral PFTs and/or species varies greatly in response to herbivory as same as that of GI or GD PFTs (or species) in the study, then net primary production, species numbers, and species components of the community should not remain stable. Two main mechanisms, the selection effect and the niche complementarity effect, can be used to explain the role of plant diversity in ecosystem resource dynamics, and were based on the presence of a range of functional traits and species within the community [5]. We found that the percentage of NE response types was highest (61%) (Table 5), and that these occupied all optimal traits (and attributes) (Appendix 2). Around 56% of international studies showed a unimodal pattern or a saturated response, in the relationship between primary production and species diversity [67]. This suggests that high and stable primary production is related to the presence of a considerable number of species, especially in natural communities. In the alpine shrub meadow at Haibei Research Station, a high and stable primary production was obtained in functional groups when there were about 10 species per group [45].

Díaz et al. [1] suggested that the best PFT prediction of community response to grazing could be achieved by combining optimal traits. Vesk et al. [15] documented weak predictability of grazing response to species abundance using a single functional trait. Among our eleven optimal PFTs, four-trait and three-trait PFTs should be the most valuable in predicting response to grazing. Of these, the PFTs Tall×Shrub×Erect×Scattered and Small×Forb×Rosette exhibited the greatest fit with axis 1 (Table 6), and are the best PFT predictors. Using this minimum PFT set, moreover, we can accurately and easily predict different directions in community dynamics because this PFT set consist of a few species. The four-trait PFT Tall×Shrub×Erect×Scattered, for example, consists of just three shrubby species (Table 6), accounting for 4.3% of all 69 species included, and showing a simple linear response model of SDR to grazing:  $Y = 2.45 - 0.13X$  ( $R^2 = 0.14$ ,  $F_{1,34} = 5.29$ ,  $P = 0.028$ ) (Appendix

2). Similarly, the response model of the three-trait PFT, Small×Forb×Rosette is  $Y = 3.01 + 0.06X$  ( $R^2 = 0.13$ ,  $F_{1,34} = 4.93$ ,  $P = 0.033$ ) (Appendix 2), also involving nine herbaceous species (Table 6). The total number of these species accounts for 13% of all 69 species. Kühner and Kleyer [18] suggested that the higher the number of species per PFT, the lower was the probability that all species really co-occurred in a plot; resulting in an insufficient estimate of a whole PFT in response to environmental variables.

It has been reported that the agronomic characteristics of the pasture can be deduced from changes in dominant functional type, and that the vegetation structure of an intensively grazed experimental area was homogeneous because competition dominance of higher productive functional types was weakened by grazing defoliation [6]. In the past 30 years, overgrazing and other anthropogenic factors has resulted in serious degradation of the alpine meadow ecosystem on the Qinghai-Tibet Plateau, with an annual rate of degradation of 6.64%–34.45% [59, 68]. In severely degraded grassland, all native shrub, sedges and grass species have disappeared [32]. Aboveground and root biomasses were only 38% and 14.7%, respectively, of those in undegraded land [32]. Long term overgrazing may thus result in the loss of productive PFTs and cause local extinctions of native species, usually of high quality forage plants and grazing-sensitive species. We found that heavy grazing intensity (i.e. 8 Tibetan sheep/ha), which may already approach or exceed the threshold value, can induce degradation of the community. The SDRs of dominant and productive PFTs, such as Tall, Tall×Shrub, Tall×Shrub×Erect and Medium×Grass×Erect, significantly declined. The SDRs of PFTs mostly unavailable for sheep and yaks, such as Small×Forb and Small×Forb×Rosette increased after heavy grazing (Figure 1). These PFTs agree with the trait attributes previously identified in the alpine meadow ecosystems of Qinghai-Tibet Plateau [24, 33–35, 40, 45, 69]. Many studies have reported a sharp decline in the aboveground biomass of shrubs, grasses, and sedges, and an obvious rise in biomass of low quality forbs or harmful weeds, as grazing density increased [31, 33–35, 69]. In this region the availability of soil nutrients was significantly decreased by heavy grazing [55, 69]. As a result, grassland quality clearly decreased over time [35]. Díaz and Cabido [5] suggested that the loss of an entire PFT could have a larger impact on ecosystem function than would occur if the same number of species were deleted from a variety of functional types. Therefore, periodic resting or decreasing grazing pressure could be a cost-efficient management strategy to favor palatable species, and productive PFTs, to maintain ecosystem function and the feed value of the grassland.

## 4 Conclusions

Identifying PFTs or a minimum set of the most important

plant traits provides a meaningful research and management tool. The plant trait perspective clearly improves our insight into mechanisms behind observed changes in species abundance following alteration in disturbance regime [64]. We clearly illustrate the advantage of optimizing traits and PFTs using multivariate analysis of trait-based data. We demonstrate that a minimum set of PFTs, resulting from an optimal four individual traits, can provide consistent predictions of community response to grazing in this region. The turnover of species, traits, and PFT composition, showing different responses to grazing along a grazing gradient, can account for community dynamics other than species diversity. Responses of the optimal PFTs, GI and GD, could be used to understand the mechanisms underlying community dynamics following grazing in alpine shrub meadow ecosystems. A large number of neutral PFTs and/or species, may be important in maintaining long-term community stability. This approach is able to link management practices to vegetation structure, and provide a basis for future large-scale plant trait comparisons.

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Appendix 1 Four single optimal traits, their attributes, and the plant species involved

Plant height		Plant inclination		Growth form		Economic group	
Tall	Erect	Plant inclination	Scattered	Growth form	Shrubs	Economic group	
<i>Deyeuxia flavens</i>	<i>Anaphalis hancockii</i>		<i>Anemone obtusiloba</i>		<i>Potentilla fruticosa</i>		
<i>Elymus nutans</i>	<i>Anaphalis lacteal</i>		<i>Astragalus</i> sp.		<i>Salix ortitrephe</i>		
<i>Gentianopsis paludosa</i>	<i>Anemone obtusiloba</i>		<i>Euphrasia pectinata</i>		<i>Spiraea alpine</i>		
<i>Helictotrichon tibeticum</i>	<i>Carex atrofuscus</i>		<i>Galium verum</i>		<b>Grasses</b>		
<i>Kobresia capillifolia</i>	<i>Carex moorcroftii</i>		<i>Gentiana aristata</i>		<i>Deyeuxia flavens</i>		
<i>Morina chinensis</i>	<i>Deyeuxia flavens</i>		<i>Gentiana lawrencei</i> , var. <i>farreri</i>		<i>Elymus nutans</i>		
<i>Notopterygium forbesii</i>	<i>Elymus nutans</i>		<i>Gentiana squarrosa</i>		<i>Festuca ovina</i>		
<i>Potentilla fruticosa</i>	<i>Euphrasia pectinata</i>		<i>Gentiana straminea</i>		<i>Festuca rubra</i>		
<i>Phragrostis concinna</i>	<i>Festuca ovina</i>		<i>Gentianopsis paludosa</i>		<i>Helictotrichon tibeticum</i>		
<i>Phragrostis dichotoma</i>	<i>Festuca rubra</i>		<i>Gueldenstaedtia diversifolia</i>		<i>Koeleria cristata</i>		
<i>Salix ortitrephe</i>	<i>Gentianopsis paludosa</i>		<i>Morina chinensis</i>		<i>Poa orinosa</i>		
<i>Spiraea alpine</i>	<i>Geranium pylzowianum</i>		<i>Notopterygium forbesii</i>		<i>Phragrostis concinna</i>		
<b>Medium</b>	<i>Helictotrichon tibeticum</i>		<i>Oxytropis ochrocephala</i>		<i>Phragrostis dichotoma</i>		
<i>Anaphalis hancockii</i>	<i>Iris goniocarpa</i>		<i>Pedicularis alaschanica</i>		<i>Stipa aliena</i>		
<i>Anaphalis lacteal</i>	<i>Kobresia capillifolia</i>		<i>Pedicularis kansuensis</i>		<b>Sedges</b>		
<i>Anemone obtusiloba</i>	<i>Kobresia humilis</i>		<i>Pedicularis</i> sp.		<i>Carex atrofuscus</i>		
<i>Aster flaccidus</i>	<i>Koeleria cristata</i>		<i>Potentilla bifurca</i>		<i>Carex moorcroftii</i>		
<i>Festuca ovina</i>	<i>Morina chinensis</i>		<i>Potentilla discolor</i>		<i>Kobresia capillifolia</i>		
<i>Festuca rubra</i>	<i>Notopterygium forbesii</i>		<i>Potentilla fruticosa</i>		<i>Kobresia humilis</i>		
<i>Koeleria cristata</i>	<i>Parnassia trinervis</i>		<i>Ranunculus hirtellus</i>		<i>Scirpus distigmaticus</i>		
<i>Ligularia sagitta</i>	<i>Poa orinosa</i>		<i>Ranunculus pulchellus</i>		<b>Legumes</b>		
<i>Ligularia virgaurea</i>	<i>Polygonum viviparum</i> L. var. <i>angustum</i>		<i>Ranunculus pulchellus</i>		<i>Astragalus</i> sp.		
<i>Poa orinosa</i>	<i>Polygonum viviparum</i>		<i>Ranunculus tanguticus</i>		<i>Gueldenstaedtia diversifolia</i>		
<i>Polygonum viviparum</i>	<i>Potentilla fruticosa</i>		<i>Salix ortitrephe</i>		<i>Oxytropis ochrocephala</i>		
<i>Stellera chamaejasme</i>	<i>Phragrostis concinna</i>		<i>Saussurea kokonorensis</i>		<i>Thermopsis lanceolata</i>		
<i>Stipa aliena</i>	<i>Phragrostis dichotoma</i>		<i>Saussurea nigrescens</i>		<b>Forbs</b>		
<i>Thermopsis lanceolata</i>	<i>Salix ortitrephe</i>		<i>Saussurea superba</i>		<i>Anaphalis hancockii</i>		
<i>Trollius farreri</i>	<i>Saxifraga montana</i>		<i>Saxifraga montana</i>		<i>Anaphalis lacteal</i>		
<b>Small</b>	<i>Scirpus distigmaticus</i>		<i>Spiraea alpine</i>		<i>Anemone obtusiloba</i>		
<i>Astragalus</i> sp.	<i>Spiraea alpine</i>		<i>Stellaria media</i>		<i>Aster flaccidus</i>		
<i>Carex atrofuscus</i>	<i>Stellaria umbellata</i>		<i>Stellaria umbellata</i>		<i>Aster flaccidus</i>		
<i>Carex moorcroftii</i>	<i>Swertia tetraptera</i>		<i>Stellera chamaejasme</i>		<i>Euphrasia pectinata</i>		
<i>Euphrasia pectinata</i>	<i>Thalictrum alpinum</i>		<i>Swertia tetraptera</i>		<i>Galium aparine</i>		
<i>Galium aparine</i>	<i>Thermopsis lanceolata</i>		<i>Taraxacum mongolicum</i>		<i>Galium verum</i>		
<i>Galium verum</i>	<i>Torularia humilis</i>		<i>Thalictrum alpinum</i>		<i>Galium verum</i>		
<i>Gentiana aristata</i>	<i>Trollius farreri</i>		<i>Thermopsis lanceolata</i>		<i>Gentiana aristata</i>		
<i>Gentiana lawrencei</i> , var. <i>farreri</i>	<i>Viola bulbosa</i>		<i>Torularia humilis</i>		<i>Gentiana lawrencei</i> , var. <i>farreri</i>		
<i>Gentiana squarrosa</i>	<b>Prostrate</b>		<b>Bunch</b>		<i>Gentiana squarrosa</i>		
<i>Gentiana straminea</i>	<i>Astragalus</i> sp.		<i>Aster flaccidus</i>		<i>Geranium pylzowianum</i>		
<i>Geranium pylzowianum</i>	<i>Galium aparine</i>		<i>Carex atrofuscus</i>		<i>Lancea tibetica</i>		
<i>Gueldenstaedtia diversifolia</i>	<i>Galium verum</i>		<i>Carex moorcroftii</i>		<i>Leontopodium longifolium</i>		
	<i>Gentiana aristata</i>		<i>Elymus nutans</i>		<i>Leontopodium nanum</i>		
					<i>Parnassia trinervis</i>		

(To be continued on the next page)

(continued)

<i>Iris goniocarpa</i>	<i>Gentiana squarrosa</i>	<i>Gentiana straminea</i>	<i>Polygonum viviparum</i> L. var. <i>angustum</i>
<i>Kobresia humilis</i>	<i>Pedicularis ataschanica</i>	<i>Geranium pylzowianum</i>	<i>Polygonum viviparum</i>
<i>Lancea tibetica</i>	<i>Pedicularis kansuensis</i>	<i>Lancea tibetica</i>	<i>Potentilla anserine</i>
<i>Leontopodium longifolium</i>	<i>Pedicularis</i> sp.	<i>Parnassia trinervis</i>	<i>Potentilla bifurca</i>
<i>Leontopodium nanum</i>	<i>Potentilla bifurca</i>	<i>Polygonum viviparum</i>	<i>Potentilla discolor</i>
<i>Oxytropis ochrocephala</i>	<i>Potentilla discolor</i>	<i>Polygonum viviparum</i> L. var. <i>angustum</i>	<i>Ranunculus hirtellus</i>
<i>Parnassia trinervis</i>	<i>Ranunculus hirtellus</i>	<i>Potentilla anserine</i>	<i>Ranunculus pulchellus</i>
<i>Pedicularis ataschanica</i>	<i>Ranunculus pulchellus</i>	<i>Rubia cordifolia</i>	<i>Rubia cordifolia</i>
<i>Pedicularis kansuensis</i>	<i>Ranunculus tanguticus</i>	<i>Scirpus distigmaticus</i>	<i>Saussurea kokonorensis</i>
<i>Pedicularis</i> sp.	<i>Rubia cordifolia</i>	<i>Trollius farreri</i>	<i>Saussurea nigrescens</i>
<i>Polygonum viviparum</i> L. var. <i>angustum</i>	<i>Stellaria media</i>	<b>Closely Bunched</b>	<i>Saussurea superba</i>
<i>Potentilla anserine</i>	<i>Stellaria umbellata</i>	<i>Anaphalis hancockii</i>	<i>Saxifraga montana</i>
<i>Potentilla bifurca</i>	<i>Stellera chamaejasme</i>	<i>Anaphalis lacteal</i>	<i>Stellaria media</i>
<i>Potentilla discolor</i>	<i>Stipa aliena</i>	<i>Deyeuxia flavens</i>	<i>Stellaria umbellata</i>
<i>Ranunculus hirtellus</i>	<b>Rosette</b>	<i>Festuca ovina</i>	<i>Swertia tetraptera</i>
<i>Ranunculus pulchellus</i>	<i>Aster flaccidus</i>	<i>Festuca rubra</i>	<i>Taraxacum mongolicum</i>
<i>Ranunculus tanguticus</i>	<i>Gentiana lawrencei</i> , var. <i>farreri</i>	<i>Helictotrichon tibeticum</i>	<i>Torularia humilis</i>
<i>Rubia cordifolia</i>	<i>Gentiana straminea</i>	<i>Iris goniocarpa</i>	<i>Trollius farreri</i>
<i>Saussurea kokonorensis</i>	<i>Guaeldenstaedtia diversifolia</i>	<i>Kobresia capitifolia</i>	<i>Viola bulbosa</i>
<i>Saussurea nigrescens</i>	<i>Lancea tibetica</i>	<i>Kobresia humilis</i>	<b>Harmful</b>
<i>Saussurea superba</i>	<i>Leontopodium longifolium</i>	<i>Koeleria cristata</i>	<i>Gentiana straminea</i>
<i>Saxifraga montana</i>	<i>Leontopodium nanum</i>	<i>Leontopodium longifolium</i>	<i>Gentianopsis paludosa</i>
<i>Scirpus distigmaticus</i>	<i>Ligularia sagitta</i>	<i>Leontopodium nanum</i>	<i>Iris goniocarpa</i>
<i>Stellaria media</i>	<i>Ligularia virgaurea</i>	<i>Ligularia sagitta</i>	<i>Ligularia sagitta</i>
<i>Stellaria umbellata</i>	<i>Oxytropis ochrocephala</i>	<i>Ligularia virgaurea</i>	<i>Ligularia virgaurea</i>
<i>Swertia tetraptera</i>	<i>Potentilla anserine</i>	<i>Poa orinosa</i>	<i>Morina chinensis</i>
<i>Taraxacum mongolicum</i>	<i>Saussurea kokonorensis</i>	<i>Ptilagrostis concinna</i>	<i>Notopterygium forbesii</i>
<i>Thalictrum alpinum</i>	<i>Saussurea nigrescens</i>	<i>Ptilagrostis dichotoma</i>	<i>Oxytropis ochrocephala</i>
<i>Torularia humilis</i>	<i>Saussurea superba</i>	<i>Stipa aliena</i>	<i>Pedicularis ataschanica</i>
<i>Viola bulbosa</i>	<i>Taraxacum mongolicum</i>	<i>Viola bulbosa</i>	<i>Pedicularis kansuensis</i>
			<i>Pedicularis</i> sp.
			<i>Ranunculus tanguticus</i>
			<i>Spiraea alpine</i>
			<i>Stellera chamaejasme</i>
			<i>Stipa aliena</i>
			<i>Thalictrum alpinum</i>
			<i>Thermopsis lanceolata</i>

Appendix 2 All the PFTs of combined traits and their response-to-grazing models<sup>a)</sup>

Tow-traits' PFTs		Three-traits' PFTs		Four-traits' PFTs	
GI		GI		GI	
1.	<b>SmxSc</b> : $Y=1.48+0.10X$ , $R^2=0.13$ , $F_{1,34}=5.17$ , $P=0.029$	1.	<b>MexErxBu</b> : $Y=1.05+0.14X$ , $R^2=0.10$ , $F_{1,34}=3.62$ , $P=0.066^*$	1.	<b>MexFoxErxBu</b> : $Y=0.69+0.13X$ , $R^2=0.12$ , $F_{1,34}=4.63$ , $P=0.039$
2.	<b>SmxFo</b> : $Y=3.57+0.05X$ , $R^2=0.24$ , $F_{1,34}=10.49$ , $P=0.003$	2.	<b>SmxSexEr</b> : $Y=1.48+0.10X$ , $R^2=0.13$ , $F_{1,34}=5.17$ , $P=0.029$	2.	<b>SmxSexErxBu</b> : $Y=0.69+0.13X$ , $R^2=0.12$ , $F_{1,34}=4.63$ , $P=0.039$
3.	<b>SmxPr</b> : $Y=2.14x^{0.05X}$ , $R^2=0.17$ , $F_{1,34}=6.74$ , $P=0.014$	3.	<b>SmxLexRo</b> : $Y=1.12+0.07X$ , $R^2=0.08$ , $F_{1,34}=2.86$ , $P=0.110^*$	3.	<b>SmxLexRoxSc</b> : $Y=1.12+0.07X$ , $R^2=0.08$ , $F_{1,34}=2.86$ , $P=0.110^*$
4.	<b>SmxRo</b> : $Y=3.15+0.06X$ , $R^2=0.13$ , $F_{1,34}=5.08$ , $P=0.031$	4.	<b>SmxFoxRo</b> : $Y=3.01+0.06X$ , $R^2=0.13$ , $F_{1,34}=4.93$ , $P=0.033$	4.	<b>SmxFoxPrxSc</b> : $Y=2.12+0.07X$ , $R^2=0.15$ , $F_{1,34}=5.86$ , $P=0.021$
5.	<b>SmxBu</b> : $Y=2.06+0.12X$ , $R^2=0.17$ , $F_{1,34}=6.96$ , $P=0.012$	5.	<b>SmxSexBu</b> : $Y=0.70+0.13X$ , $R^2=0.12$ , $F_{1,34}=4.63$ , $P=0.039$	5.	<b>SmxFoxRoxCl</b> : $Y=1.60-0.001X$ , $R^2=0.10$ , $F_{1,34}=3.96$ , $P=0.055^*$
6.	<b>SexBu</b> : $Y=0.70+0.13X$ , $R^2=0.17$ , $F_{1,34}=6.96$ , $P=0.012$	6.	<b>SmxFoxPr</b> : $Y=2.14+0.07X$ , $R^2=0.16$ , $F_{1,34}=6.40$ , $P=0.016$	6.	<b>SmxFoxRoxBu</b> : $Y=1.18+0.18X$ , $R^2=0.25$ , $F_{1,34}=11.31$ , $P=0.002$
7.	<b>FoxPr</b> : $Y=2.10x^{0.05X}$ , $R^2=0.16$ , $F_{1,34}=6.61$ , $P=0.015$	7.	<b>SmxFoxCl</b> : $Y=2.18-0.001X$ , $R^2=0.10$ , $F_{1,34}=3.86$ , $P=0.058$	GD	
8.	<b>FoxBu</b> : $Y=3.06+0.05X$ , $R^2=0.13$ , $F_{1,34}=5.15$ , $P=0.030$	8.	<b>SmxFoxxBu</b> : $Y=1.77+0.13X$ , $R^2=0.15$ , $F_{1,34}=5.98$ , $P=0.020$	1.	<b>TaxShxErSc</b> : $Y=2.45-0.13X$ , $R^2=0.14$ , $F_{1,34}=5.29$ , $P=0.028$
9.	<b>FoxBu</b> : $Y=2.06+0.13X$ , $R^2=0.20$ , $F_{1,34}=8.37$ , $P=0.007$	9.	<b>SmxPrxSc</b> : $Y=2.16+0.07X$ , $R^2=0.15$ , $F_{1,34}=6.06$ , $P=0.019$	2.	<b>MexGrxErxCi</b> : $Y=2.17-0.09X$ , $R^2=0.11$ , $F_{1,34}=4.16$ , $P=0.049$
10.	<b>ErxBu</b> : $Y=2.24x(1.02)^X$ , $R^2=0.08$ , $F_{1,34}=2.89$ , $P=0.098^*$	10.	<b>SmxRoxCl</b> : $Y=2.08-0.001X$ , $R^2=0.10$ , $F_{1,34}=3.96$ , $P=0.055^*$	3.	<b>MexLexErSc</b> : $Y=1.06-0.18X$ , $R^2=0.24$ , $F_{1,34}=10.86$ , $P=0.002$
11.	<b>PrxSc</b> : $Y=2.12x(1.03)^X$ , $R^2=0.16$ , $F_{1,34}=6.35$ , $P=0.017$	11.	<b>SmxRoxxBu</b> : $Y=1.40+0.16X$ , $R^2=0.22$ , $F_{1,34}=9.69$ , $P=0.004$	NE	
12.	<b>RoxBu</b> : $Y=1.40+0.16X$ , $R^2=0.22$ , $F_{1,34}=9.69$ , $P=0.004$	12.	<b>HaxErxSc</b> : $Y=2.40e^{-0.3X}$ , $R^2=0.10$ , $F_{1,34}=3.95$ , $P=0.055$	1.	<b>TaxGrxErxCi</b> : 2. <b>TaxGrxErxBu</b> : 3. <b>TaxSexErxCi</b> : 4.
GD		13.	<b>TaxShxEr</b> : $Y=2.45-0.13X$ , $R^2=0.14$ , $F_{1,34}=5.29$ , $P=0.028$	1.	<b>TaxHaxErSc</b> : 5. <b>MexGrxErxCi</b> : 6. <b>MexFoxErxCi</b> : 7.
1.	<b>TaxSh</b> : $Y=2.45-0.13X$ , $R^2=0.14$ , $F_{1,34}=5.29$ , $P=0.028$	14.	<b>FoxPrxBu</b> : $Y=1.12+0.07X$ , $R^2=0.08$ , $F_{1,34}=2.86$ , $P=0.110^*$	2.	<b>MexHaxErSc</b> : 8. <b>MexFoxRoxBu</b> : 9. <b>MexHaxPrxCi</b> : 10.
2.	<b>TaxEr</b> : $Y=2.99-0.13X$ , $R^2=0.18$ , $F_{1,34}=7.550$ , $P=0.010$	15.	<b>FoxPrxSc</b> : $Y=2.12+0.07X$ , $R^2=0.15$ , $F_{1,34}=5.86$ , $P=0.021$	3.	<b>MexHaxPrxSc</b> : 11. <b>MexHaxRoxCl</b> : 12. <b>SmxSexErxCi</b> : 13.
3.	<b>TaxSc</b> : $Y=2.54-0.13X$ , $R^2=0.14$ , $F_{1,34}=5.47$ , $P=0.025$	16.	<b>FoxRoxBu</b> : $Y=1.40+0.16X$ , $R^2=0.22$ , $F_{1,34}=9.69$ , $P=0.004$	4.	<b>SmxLexPrxSc</b> : 14. <b>SmxFoxErxCi</b> : 15. <b>SmxFoxRoxBu</b> : 16.
4.	<b>MexGr</b> : $Y=2.72-0.08X$ , $R^2=0.18$ , $F_{1,34}=7.67$ , $P=0.009$	17.	<b>HaxErxSc</b> : $Y=2.40e^{-0.3X}$ , $R^2=0.10$ , $F_{1,34}=3.95$ , $P=0.055$	5.	<b>SmxFoxErSc</b> : 17. <b>SmxFoxPrxBu</b> : 18. <b>SmxFoxRoxSc</b> : 19.
5.	<b>MexLe</b> : $Y=1.06-0.18X$ , $R^2=0.24$ , $F_{1,34}=10.86$ , $P=0.002$	GD		6.	<b>SmxHaxErxCi</b> : 20. <b>SmxHaxErxSc</b> : 21. <b>SmxHaxRoxSc</b>
6.	<b>MexHa</b> : $Y=2.31-0.14X$ , $R^2=0.12$ , $F_{1,34}=4.83$ , $P=0.035$	1.	<b>TaxShxEr</b> : $Y=2.45-0.13X$ , $R^2=0.14$ , $F_{1,34}=5.29$ , $P=0.028$	1.	<b>TaxShxEr</b> : $Y=2.45-0.13X$ , $R^2=0.14$ , $F_{1,34}=5.29$ , $P=0.028$
7.	<b>ShxEr</b> : $Y=2.45-0.13X$ , $R^2=0.14$ , $F_{1,34}=5.29$ , $P=0.028$	2.	<b>TaxShxSc</b> : $Y=2.45-0.13X$ , $R^2=0.14$ , $F_{1,34}=5.289$ , $P=0.028$	2.	<b>TaxErxSc</b> : $Y=2.54-0.13X$ , $R^2=0.14$ , $F_{1,34}=5.47$ , $P=0.025$
8.	<b>ShxSc</b> : $Y=2.45-0.13X$ , $R^2=0.14$ , $F_{1,34}=5.29$ , $P=0.028$	3.	<b>TaxErxSc</b> : $Y=2.54-0.13X$ , $R^2=0.14$ , $F_{1,34}=5.47$ , $P=0.025$	3.	<b>MexGrxEr</b> : $Y=2.17-0.09X$ , $R^2=0.11$ , $F_{1,34}=4.16$ , $P=0.049$
9.	<b>GrxEr</b> : $Y=2.38-0.07X$ , $R^2=0.19$ , $F_{1,34}=7.71$ , $P=0.009$	4.	<b>MexGrxEr</b> : $Y=2.17-0.09X$ , $R^2=0.11$ , $F_{1,34}=4.16$ , $P=0.049$	4.	<b>MexLexEr</b> : $Y=1.06-0.18X$ , $R^2=0.24$ , $F_{1,34}=10.86$ , $P=0.002$
10.	<b>GrxCi</b> : $Y=2.78-0.07X$ , $R^2=0.20$ , $F_{1,34}=8.29$ , $P=0.007$	5.	<b>MexHaxEr</b> : $Y=1.06-0.18X$ , $R^2=0.24$ , $F_{1,34}=10.86$ , $P=0.002$	5.	<b>MexGrxCi</b> : $Y=2.72-0.08X$ , $R^2=0.18$ , $F_{1,34}=7.67$ , $P=0.009$
11.	<b>LexEr</b> : $Y=1.06-0.18X$ , $R^2=0.24$ , $F_{1,34}=10.86$ , $P=0.002$	6.	<b>MexHaxEr</b> : $Y=1.06-0.18X$ , $R^2=0.24$ , $F_{1,34}=10.86$ , $P=0.002$	6.	<b>MexLexSc</b> : $Y=1.05-0.17X$ , $R^2=0.23$ , $F_{1,34}=10.03$ , $P=0.003$
12.	<b>HaxEr</b> : $Y=2.45x(0.97)^X$ , $R^2=0.08$ , $F_{1,34}=2.91$ , $P=0.097^*$	7.	<b>MexGrxCi</b> : $Y=2.72-0.08X$ , $R^2=0.18$ , $F_{1,34}=7.67$ , $P=0.009$	7.	<b>MexHaxSc</b> : $Y=1.06-0.17X$ , $R^2=0.23$ , $F_{1,34}=10.03$ , $P=0.003$
13.	<b>HaxPr</b> : $Y=1.80-0.06lnX$ , $R^2=0.08$ , $F_{1,34}=2.91$ , $P=0.097^*$	8.	<b>MexLexSc</b> : $Y=1.05-0.17X$ , $R^2=0.23$ , $F_{1,34}=10.03$ , $P=0.003$	8.	<b>ShxErSc</b> : $Y=2.45-0.136X$ , $R^2=0.14$ , $F_{1,34}=5.29$ , $P=0.028$
14.	<b>ErxCi</b> : $Y=2.89-0.05lnX$ , $R^2=0.16$ , $F_{1,34}=6.25$ , $P=0.017$	9.	<b>MexHaxSc</b> : $Y=1.06-0.17X$ , $R^2=0.23$ , $F_{1,34}=10.03$ , $P=0.003$	9.	<b>GrxErxCi</b> : $Y=2.28-0.07X$ , $R^2=0.17$ , $F_{1,34}=7.02$ , $P=0.012$
15.	<b>ErxSc</b> : $Y=3.31-0.08X$ , $R^2=0.16$ , $F_{1,34}=6.59$ , $P=0.015$	10.	<b>ShxErSc</b> : $Y=2.45-0.136X$ , $R^2=0.14$ , $F_{1,34}=5.29$ , $P=0.028$	10.	<b>LexErxSc</b> : $Y=2.61-0.10X$ , $R^2=0.11$ , $F_{1,34}=4.17$ , $P=0.049$
NE		11.	<b>ShxErSc</b> : $Y=2.45-0.136X$ , $R^2=0.14$ , $F_{1,34}=5.29$ , $P=0.028$	11.	<b>LexErxSc</b> : $Y=2.61-0.10X$ , $R^2=0.11$ , $F_{1,34}=4.17$ , $P=0.049$
1.	<b>TaxGr</b> : 2. <b>TaxSc</b> : 3. <b>TaxHa</b> : 4. <b>TaxCl</b> : 5. <b>TaxBu</b> : 6. <b>MexFo</b> : 7. 12.	12.	<b>GrxErxCi</b> : $Y=2.28-0.07X$ , $R^2=0.17$ , $F_{1,34}=7.02$ , $P=0.012$	12.	<b>LexErxSc</b> : $Y=2.61-0.10X$ , $R^2=0.11$ , $F_{1,34}=4.17$ , $P=0.049$
<b>MexEr</b> : 8. <b>Me xPr</b> : 9. <b>MexRo</b> : 10. <b>MexCl</b> : 11. <b>MexBu</b> : 12. 13.	13.	<b>LexErxSc</b> : $Y=2.61-0.10X$ , $R^2=0.11$ , $F_{1,34}=4.17$ , $P=0.049$	13.	<b>LexErxSc</b> : $Y=2.61-0.10X$ , $R^2=0.11$ , $F_{1,34}=4.17$ , $P=0.049$	
<b>MexSc</b> : 13. <b>SmxLe</b> : 14. <b>SmxHa</b> : 15. <b>SmxEr</b> : 16. <b>SmxCi</b> : 17. <b>NE</b>	14.	<b>LexErxSc</b> : $Y=2.61-0.10X$ , $R^2=0.11$ , $F_{1,34}=4.17$ , $P=0.049$	14.	<b>LexErxSc</b> : $Y=2.61-0.10X$ , $R^2=0.11$ , $F_{1,34}=4.17$ , $P=0.049$	
<b>SmxSc</b> : 18. <b>GrxPr</b> : 19. <b>GrxBu</b> : 20. <b>SexEr</b> : 21. <b>SexCl</b> : 22. <b>LexPr</b> :	15.	<b>LexErxSc</b> : $Y=2.61-0.10X$ , $R^2=0.11$ , $F_{1,34}=4.17$ , $P=0.049$	15.	<b>LexErxSc</b> : $Y=2.61-0.10X$ , $R^2=0.11$ , $F_{1,34}=4.17$ , $P=0.049$	
<b>MexSc</b> : 23. <b>LexRo</b> : 24. <b>LexSc</b> : 25. <b>FoxEr</b> : 26. <b>FoxCl</b> : 27. <b>FoxSc</b> : 28. <b>RoxCl</b> :	16.	<b>LexErxSc</b> : $Y=2.61-0.10X$ , $R^2=0.11$ , $F_{1,34}=4.17$ , $P=0.049$	16.	<b>LexErxSc</b> : $Y=2.61-0.10X$ , $R^2=0.11$ , $F_{1,34}=4.17$ , $P=0.049$	
<b>HaxPr</b> : 29. <b>HaxRo</b> : 30. <b>HaxSc</b> : 31. <b>PrxCi</b> : 32. <b>PrxBu</b> : 33. <b>RoxCl</b> :	17.	<b>LexErxSc</b> : $Y=2.61-0.10X$ , $R^2=0.11$ , $F_{1,34}=4.17$ , $P=0.049$	17.	<b>LexErxSc</b> : $Y=2.61-0.10X$ , $R^2=0.11$ , $F_{1,34}=4.17$ , $P=0.049$	
34. <b>RoxSc</b>	18.	<b>LexErxSc</b> : $Y=2.61-0.10X$ , $R^2=0.11$ , $F_{1,34}=4.17$ , $P=0.049$	18.	<b>LexErxSc</b> : $Y=2.61-0.10X$ , $R^2=0.11$ , $F_{1,34}=4.17$ , $P=0.049$	

a) Data are referred to as marginally significant for  $0.05 < P < 0.10$ . PFT was defined as a possible combination of attributes of four optimal traits; and using between two and four traits. Optimal traits (and attributes) include growth form (Closely Bunched, Scattered), plant inclination (Erect, Prostrate, Rosette), economic group (Shrub, Grass, Sedge, Legume, Forb, Harmful) and mature plant height (Tall, Medium, Small). Combinations of abbreviated boldface letter indicate a PFT. Three types of grazing response were found: GI = grazing increaser; GD = grazing decrease; NE = neutral.