

## Linking grazing response of species abundance to functional traits in the Tibetan alpine meadow

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**Abstract** Whether grazing response of species abundance can be predicted by plant functional trait remains a challenge untested in a specific ecosystem. We measured species abundance and relevant functional traits for 30 common component species in a moderately grazed and a control community over 3 years (2005, 2006 and 2007) in a *Kobresia capillifolia* dominated alpine meadow on the Tibetan Plateau. Our objective was to examine species response to grazing and to test the relationship between the response of species abundance and functional traits in grazed and control habitats. Our results showed: i) in terms of species relative abundance and saturated height (the maximum height of an adult

individual), most component species significantly decrease in response to moderate grazing and the effect differed among species and between functional groups. ii) The response of species abundance was significantly negatively correlated with saturated height, but not correlated with specific leaf area or seed size. We concluded that the response direction of species abundance to grazing can be predicted by functional traits, whereas it is a weak predictor of the extent of grazing response in species abundance.

**Keywords** Functional groups · Leaf-Height-Seed scheme · Saturated height · Seed size · Specific leaf area · Tibetan Plateau

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### Introduction

Linking plant community composition and individual component species response to grazing is a central topic in basic plant ecology as well as in rangeland management (McNaughton 1985; Moog et al. 2005; Gibson 2009). Plant species can respond to grazing with adjustments in their ecophysiological traits and changes in their relative abundance (Diaz et al. 2007). Theoretically, the plant trait-based life historical strategy should take into consideration the abundance response at population or species level across variable environments (Westoby 1998; Grime 2001; Westoby et al. 2002). With the appeal of *rebuilding community ecology from functional traits* (McGill et al. 2006;

Westoby and Wright 2006), the explanation and prediction of the response of plant community and species abundance to grazing by functional trait has recently gained renewed interest (Diaz et al. 2001; Veski and Westoby 2001; Pakeman 2004; Devineau and Fournier 2005; Diaz et al. 2007; Meers et al. 2008).

Westoby et al. (1999) argued that specific leaf area (SLA), saturated height (Hs) and seed size (SS) are the three main predictors for the response of species abundance to disturbance under the Leaf-Height-Seed scheme of plant ecological strategy (Westoby 1998). According to their hypothesis, under low or moderate grazing intensity, tall plants with high SLA should decrease in their relative abundance in response to grazing due to selective grazing, while short plants with low SLA should increase in relative abundance and predominate in a grazed community (Westoby et al. 1999; Diaz et al. 2001; Cingolani et al. 2005). SS also relates to species response to grazing (Westoby 1998; Diaz et al. 2007). Diaz et al. (2001) tested this model in a herbaceous communities of subhumid grasslands in Argentina and Israel. They confirmed that grazing responses in species abundance could be predicted from simple measurable functional traits. However, after meta-analysis for the published data in Australian dry shrublands and woodlands, Veski et al. (2004) documented that the predictability of grazing responses in species abundance by functional traits is weak and much may depend on the rangeland ecosystem. They appealed for more empirical studies in specific ecosystems to address the link between functional traits and species abundance in response to grazing (Veski et al. 2004). Subsequently, several studies investigated the relationship between functional traits and the direction of species abundance response to grazing in Europe, North America and Australia (Kahmen et al. 2002; Cingolani et al. 2005; De Bello et al. 2005; Devineau and Fournier 2005; Diaz et al. 2007; Kühner and Kleyer 2008; Klimesova et al. 2008; Meers et al. 2008). Although the studies investigated ecosystems ranging from West African savanna to semi-arid Australian shrublands to sub-humid grasslands in Argentina and Israel, their conclusions were inconsistent. Whether functional traits can predict the responses of species abundance and community structure to grazing remains unclear.

We believe that this is partly due to: (i) Empirical data directly linking functional trait and the extent to which species abundance responds to grazing is still scarce; (ii)

To our knowledge, no study compares the linkage between the response of species abundance and functional traits in grazed and control habitats. Although the importance of plasticity of plant functional traits following grazing has been repeatedly documented in many publications (Louault et al. 2005; Moog et al. 2005), its link with species abundance response was often neglected by previous studies. Therefore it is necessary to test functional trait in which habitat is more suitable in predicting the response of species abundance. Moreover, there are few empirical studies testing this linkage in alpine meadows.

As reported in our previous work (Niu et al. 2009), moderate grazing significantly decreased the canopy height and the aboveground biomass, whereas there was increased species richness and photosynthetic active radiation on the soil surface. The change in community attribute was generally due to the pronounced response of graminoids to grazing. Here, we further examined the extent to which species specific response to grazing in relative abundance can be explained by key functional trait in the alpine meadow of the Tibetan Plateau. We measured species abundance and relevant functional traits for 30 common component species in a moderately grazed and control community over 3 years in order to test whether the grazing response of species abundance can be predicted by functional traits by linking the response extent of species abundance to grazing to key functional traits—SLA, Hs and SS—in a contrasted grazed and a control community. We asked the following questions:

- (1) Do functional groups differ in their responses to moderate grazing in terms of species relative abundance and functional traits?
- (2) Can the grazing response of species abundance be explained by plant functional traits as predicted by the Leaf-Height-Seed scheme of plant ecological strategy?

## Material and methods

### Study site

The experiment was on a large flat area dominated by alpine grassland in MaQu (N33°59', E102°00'), in the province of Gansu, China. The site is located in the

eastern part of the Tibetan Plateau, at 3,500 m above sea level. The mean annual temperature (MAT) is 1.2°C, ranging from -10°C in January to 11.7°C in July, with approximately 270 days of frost per year. Mean annual precipitation (MAP), measured over the last 35 years, is 620 mm, occurring mainly during the short, cool summer. During the years of the study, the MAP was 672 mm (2005), 643 mm (2006) and 592 mm (2007). The vegetation is typical alpine meadow dominated by *Kobresia capillifolia* (Cyperaceae), *Poa chalaraantha* (Poaceae), *Roegneria nutans* (Poaceae), *Stipa aliena* (Poaceae) and *Anemone obtusiloba* (Ranunculaceae). The average aboveground biomass is 60–120 g dry mass per square meter. Typically, there are 20–40 vascular plant species and 800–1,000 individual plants per square meter.

#### Experimental design

A 13 ha flat area was enclosed within 58 ha of fenced grassland in October 1999, with grazing was allowed within the enclosure only during the non-productive winter months. Outside of the enclosure (45 ha), vegetation was grazed by ungulates, with 110 yaks and 2,200 sheep grazing during all months except for 40 days between July and mid-August when the animals were moved to high-altitude pastures. The grazing was considered as moderate stocking (Li and Zhou 1998). Productivity, soil and light resources in each community were detailed previously (Niu et al. 2009).

In late May 2005, ten 5×8 m plots, separated by 2–16 m, were randomly established both within and outside the enclosure, as control and grazed treatments, respectively. Each plot was divided into two parts: a 5×5 m subplot for plant individual trait sampling, and a 5×3 m subplot for plant abundance measurement.

#### Species abundance measurements

In the middle of September, 2005, 2006 and 2007, a 0.5×0.5 m quadrat located at different places each year, was harvested from the 5×3 m subplot of each plot. The number of individuals and ramets of clonal species were recorded (Cheplick 1989; Luo et al. 2006; Niu et al. 2008) before being clipped and brought to the laboratory. Only aboveground parts were collected because the sampling of individual

root systems was deemed impossible in the dense meadow.

#### Individual trait measurements

Based on previous studies, we chose 30 common species for functional trait measurement (see Table 1). These species accounted for 70–90% of the above-ground biomass and the vegetation cover. The species were split into two functional groups: forbs and graminoids. In August of 2005 and 2006, we randomly sampled one mature leaf for each of the 30 species in each 5×5 m subplot to measure SLA. The leaf was scanned for measuring leaf area in field before being dried at 80°C for 48 h and weighed for biomass to the nearest 10<sup>-4</sup> g. In September of 2006 and 2007, we randomly measured the maximum height of 2–3 mature individuals (H<sub>s</sub>) for each of the 30 species in each 5×5 m subplot (Cornelissen et al. 2003). The measurements were conducted at fruiting time. In grazed plots, we selected individuals that were not grazed. We collected approximately 500 mature seeds from 20–30 individuals for each species in the control fenced site over the 3 years. Three replicates of 100 dried seeds were weighed for each species to measure seed mass (indicates SS) per 100 seeds.

#### Data analysis

We calculated the species relative abundance (SRA) of each component species in each quadrat as a ratio of the individual number of a given species to the total individual number of all species in the quadrat. We also measured SLA as a ratio of leaf area to dry leaf mass. Then, we estimated the means of SS, SLA and H<sub>s</sub> for each species in a grazed and a control community, with 3, 10 and 25–30 replicates, respectively.

We estimated the grazing response of species relative abundance with the log response ratio (LRR). The response of species relative abundance (RSRA)= $\log(SRAg/SRAc)$ , where SRAg and SRAc are the mean SRA for the ten quadrats of grazed and control plots, respectively. Thus, a positive RSRA value indicates that grazing increases relative abundance of a given species.

We used an independent-sample t-test to test: i) the effect of grazing on functional traits for each species; ii) the effect of grazing on forbs and graminoids in

**Table 1** The effect of grazing on component species in terms of species relative abundance and functional traits. (FG functional group, G Graminoids, F Forbs; the data indicates the mean of traits—SS Seed size (mg, n=3); SLA specific leaf area ( $\text{cm}^2/\text{mg}$ , n=7–10); Hs saturated height (cm, n=25–30);

Species	FG	2005			2006						2007					
		RSRA	SLA		SS	RSRA	SLA		Hs		SS	RSRA	Hs		SS	
			C	G			C	G	C	G			C	G		
<i>Agrostis hugoniana</i>	G	-2.30	2.2	2.5	12.9	-1.39	2.3	2.5	<b>51.7</b>	<b>2.6</b>	12.2	2.12	<b>42.9</b>	<b>3.0</b>	12.6	
<i>Agrostis micrantha</i>	G	-1.10	2.0	2.6	15.4	-0.81	3.4	4.2	<b>56.3</b>	<b>30.2</b>	14.7	0.80	<b>56.6</b>	<b>24.6</b>	151	
<i>Ajania tenuifolia</i>	F				0.00		1.6	1.9	<b>30.2</b>	<b>4.4</b>	7.8					
<i>Allium sikkimense</i>	G	-2.20	1.1	1.1	76.8	-1.75	1.6	1.7	<b>33.9</b>	<b>1.8</b>	73	-2.83	<b>29.3</b>	<b>2.9</b>	67	
<i>Anemone obtusiloba</i>	F	-1.13	<b>7.6</b>	<b>2.7</b>	195.9	-0.49	<b>6.3</b>	<b>3.1</b>	<b>22.4</b>	<b>3.1</b>	193.3	-0.61	<b>18.8</b>	<b>3.1</b>	203.4	
<i>Anemone rivularis</i> var. <i>floreminors</i>	F	0.00	2.1	2.1	480.4	0.33	2.9	2.1	<b>52.4</b>	<b>2.1</b>	488.3	-0.88	<b>48.2</b>	<b>4.8</b>	474	
<i>Bupleurum smithii</i> var. <i>parvifolium</i>	F	-1.39	2.6	2.4	25.5	-0.29	2.5	3.5	<b>34.4</b>	<b>3.6</b>	19.9	-2.13	<b>35.9</b>	<b>4.6</b>	20.9	
<i>Carum carvi</i>	F	1.39	2.3	2.3	151	2.08	3.0	2.2	<b>22.4</b>	<b>2.2</b>	176.1	0.29	<b>21.1</b>	<b>3.0</b>	186.2	
<i>Delphinium kamaonense</i> var. <i>glabrescens</i>	F	-1.61	2.6	2.8	50.6	-0.15	2.7	2.8	<b>49.3</b>	<b>3.0</b>	52	-0.55	<b>42.9</b>	<b>4.7</b>	51.4	
<i>Elymus nutans</i>	G	-0.44	1.1	1.7	348.8	-0.93	2.2	2.5	<b>78.3</b>	<b>4.5</b>	351.2	0.01	<b>56.1</b>	<b>9.1</b>	368.7	
<i>Euphorbia micractina</i>	F	-0.73	3.0	2.2	149.3	0.45	3.7	4.1	<b>25.6</b>	<b>4.7</b>	143.2	-0.47	<b>58.1</b>	<b>4.5</b>	139	
<i>Festuca sinensis</i>	G	-0.69	1.6	1.4	118.8	-1.95	2.2	2.0	<b>66.6</b>	<b>2.1</b>	122.5	-1.39	<b>33.2</b>	<b>9.8</b>	113	
<i>Gentianopsis paludosa</i>	F	1.79	4.3	4.5	12.2	1.18	5.1	2.4	<b>32.5</b>	<b>3.0</b>	13.3	1.01	<b>34.1</b>	<b>2.1</b>	14	
<i>Geranium pyrenaicum</i>	F	-1.25	3.0	3.2	277.3	2.08	1.0	3.0	<b>13.1</b>	<b>3.0</b>	275.9					
<i>Halenia elliptica</i>	F	0.96	4.3	4.6	134.5	-0.56	4.1	5.2	33.1	30.0	134.8					
<i>Kobresia capillifolia</i>	G	0.01	0.7	1.0	151.8	-0.46	0.9	0.7	<b>20.8</b>	<b>0.7</b>	129.7	-0.66	29.2	22.4	133.6	
<i>Koeleria litvinowii</i>	G	-0.69	1.7	1.6	24.7	-1.00	2.3	2.3	<b>62.4</b>	<b>2.4</b>	25.3	-2.03	<b>41.6</b>	<b>9.7</b>	22.3	
<i>Ligularia virgaurea</i>	F	-1.79	2.0	0.4	121.3	-0.60	1.6	1.5	<b>63.9</b>	<b>1.6</b>	124.2	2.53	<b>61.4</b>	<b>3.2</b>	128.3	
<i>Poa chalaraantha</i>	G	-2.25	1.7	1.4	14	-1.28	1.9	1.3	<b>59.6</b>	<b>1.3</b>	10.1	-1.89	<b>49.7</b>	<b>6.9</b>	12.2	
<i>Poa pratensis</i>	G	0.001	<b>3.6</b>	<b>2.5</b>	21.2	0.69	3.2	2.1	<b>53.7</b>	<b>2.1</b>	22.1					
<i>Potentilla saundersiana</i> var. <i>caespitosa</i>	F	0.15	2.1	1.8	36	0.71	2.0	2.2	<b>28.8</b>	<b>2.3</b>	35.6	-0.56	<b>34.5</b>	<b>3.9</b>	34.3	
<i>Ranunculus tanguticus</i>	F	0.22	2.6	2.2	28.1	-0.69	3.2	3.3	<b>25.6</b>	<b>3.3</b>	29.4	-0.59	<b>30.7</b>	<b>4.8</b>	26.4	
<i>Ranunculus tanguticus</i> var. <i>capillaceus</i>	F	-0.69	3.3	4.0	18.6	2.37	<b>3.0</b>	<b>6.1</b>	<b>22.4</b>	<b>5.2</b>	18.2	-0.03	<b>27.7</b>	<b>2.8</b>	17.8	
<i>Roegneria nutans</i>	G	0.42	1.1	1.2	324.8	-0.57	2.0	2.0	<b>68.6</b>	<b>5.0</b>	341.6	-0.75	<b>53.1</b>	<b>18.1</b>	336.8	
<i>Saussurea hieracoides</i>	F	0.69	2.3	2.1	122.5	0.29	1.5	2.5	<b>32.1</b>	<b>2.5</b>	132.9	0.76	<b>28.7</b>	<b>7.3</b>	135.4	
<i>Saussurea nigrescens</i>	F	1.50	3.2	2.5	202	-0.54	3.2	3.2	<b>27.3</b>	<b>3.2</b>	194.1	-0.77	<b>28.7</b>	<b>3.3</b>	192	
<i>Stipa aliena</i>	G	0.04	0.7	1.0	270.2	-0.12	1.5	1.7	<b>65.5</b>	<b>4.7</b>	263.7	-0.73	<b>50</b>	<b>6.5</b>	269.1	
<i>Swertia bimaculata</i>	F					1.70	3.4	4.2	<b>21.8</b>	<b>4.1</b>	15.4					
<i>Taraxacum maurocarpum</i>	F	0.49	3.5	2.9	94.8	0.29	4.3	4.1	<b>35.5</b>	<b>4.4</b>	94.2	0.83	<b>41.9</b>	<b>4.3</b>	89.1	
<i>Veronica eriogyne</i>	F	-2.30	2.4	2.7	5.2	-0.41	4.9	4.1	<b>30.4</b>	<b>4.4</b>	5.1	-2.15	<b>41.1</b>	<b>5.3</b>	5.5	

terms of species relative abundance and functional traits; iii) the difference between forbs and graminoids in RSRA and functional traits within the grazed and control community.

We performed linear regression modeling to test the relationship between RSRA and individual func-

ditional traits (transferred with Log) in the grazed and control community over 3 years. Using data from 2006, we employed a stepwise multiple regressions to further evaluate the relationship between RSRA and combinations of functional traits. All variables met the assumption of normality and homogeneity of

variances when tested using the Shapiro-Wilk *test* and Levene's *test*, respectively.

All statistical analyses were preformed in R (R Development Core Team 2009).

## Results

### Effects of grazing on species abundance and functional traits

Grazing effects were greater for graminoids than forbs, but differences were significant only in 2006 (Fig. 1a). Under grazing, the relative abundance of most species tended to decrease (negative RSRA) with a more pronounced effect in graminoids than in forbs (Table 1). The relative abundance of several forbs (e.g. *Saussurea hieracioides* and *Taraxacum maurocarpum*) increased in each of the 3 years, while any increase in the relative abundance of graminoids (e.g. *Roegneria nutans* and *Poa pratensis*) was limited to a single year (Table 1). SLA increased with grazing for some species. This was significant for one species in only 1 year (*Ranunculus tanguticus* var. *capillaceus* in 2006), while there was a significant decrease in SLA for *Anemone obtusiloba* in 2005, 2006 and for *Poa pratensis* in 2005 (Table 1). We found neither forbs nor graminoids had significant response to grazing in terms of SLA over the 2 years (Fig. 1b), whereas, almost all of the 30 species significantly decreased in saturated height after grazing in 2006 and 2007 (Table 1). Species saturated height decreased following grazing for both graminoids and forbs (Fig. 1c).

There was no significant difference in seed size between forbs and graminoids over the 3 years (data not shown).

### The relationship between the response of species abundance and functional trait

Overall, the linkage between RSRA and saturated height (Fig. 2a and c), SLA (Fig. 2b and d) and seed size ( $R_{2005}^2=0.07$ ,  $p_{2005}=0.23$ ;  $R_{2006}^2=0.06$ ,  $p_{2006}=0.98$ ;  $R_{2007}^2=0.03$ ,  $p_{2007}=0.44$ ) is very weak, although we found RSRA significantly negatively correlated with saturated height in the control community (Fig. 2c), and weakly positively correlated with SLA in the grazed community in 2006 (Fig. 2b). The multiple regressions

further showed that the correlation between RSRA and Hs in 2006 did not significantly change by combination of SLA and SS ( $R_{control}^2=0.37$ ,  $p_{control}=0.007$ ;  $R_{grazed}^2=0.19$ ,  $p_{grazed}=0.14$ ). Furthermore, no relationship between SLA, saturated height and seed size was observed in the control or the grazed community when tested using data from 2006 (data not shown).

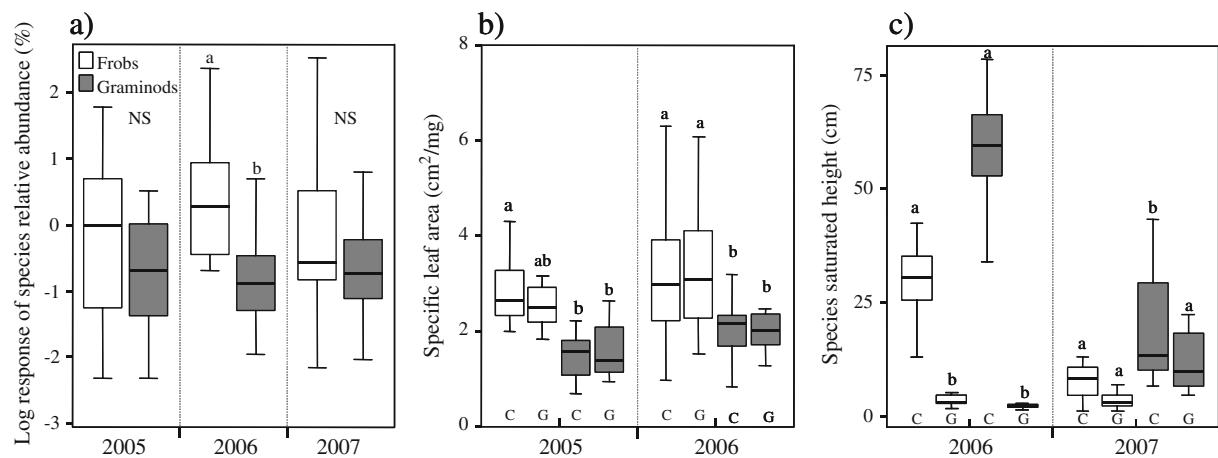
## Discussion

### Plant specific response to grazing

Species life history strategy and plant life form are among the most important predictors for species in variable environments, especially when plant community experiences repeated seasonal grazing (Bazzaz 1996; Bullock et al. 2001). Consistent with other studies investigating species relative abundance, our results indicated that grazing responses are different between functional groups and among component species (Reviewed in Diaz et al. 2007). Several graminoid species negatively responded to grazing, whereas most forbs were generally neutral (Table 1). As addressed in other studies (McIntyre and Lavorel 2001; Reviewed in Diaz et al. 2007), this specific response can be easily transferred to the level of functional groups (Fig. 2a). It is the unequal effect resulting from selective grazing pressure that caused the inconsistent grazing response between functional groups and among component species under moderate grazing (Milchunas et al. 1988; Edwards and Crawley 1999; Gibson 2009).

Decreasing of Hs and SLA has been proposed as an effective ecological strategy for avoiding be grazed and increasing resistance to grazing in grazed habitat with low competition for light and continuous disturbance (Shipley 1995; Crawley 1997; Van Der Wal et al. 2000; Falster and Westoby 2003). This was supported by previous studies (Bazzaz et al. 1987; Anderson and Frank 2003) as well as our own study which showed plant response to grazing by increasing its reproductive allocation at the expense of leaf and stem allocation (Niu et al. 2009; Zhao et al. 2009).

Although the direction of the response was similar among component species because of similar disturbance and growth limitation experienced, the response extent was significantly different among them for specific functional traits and life history



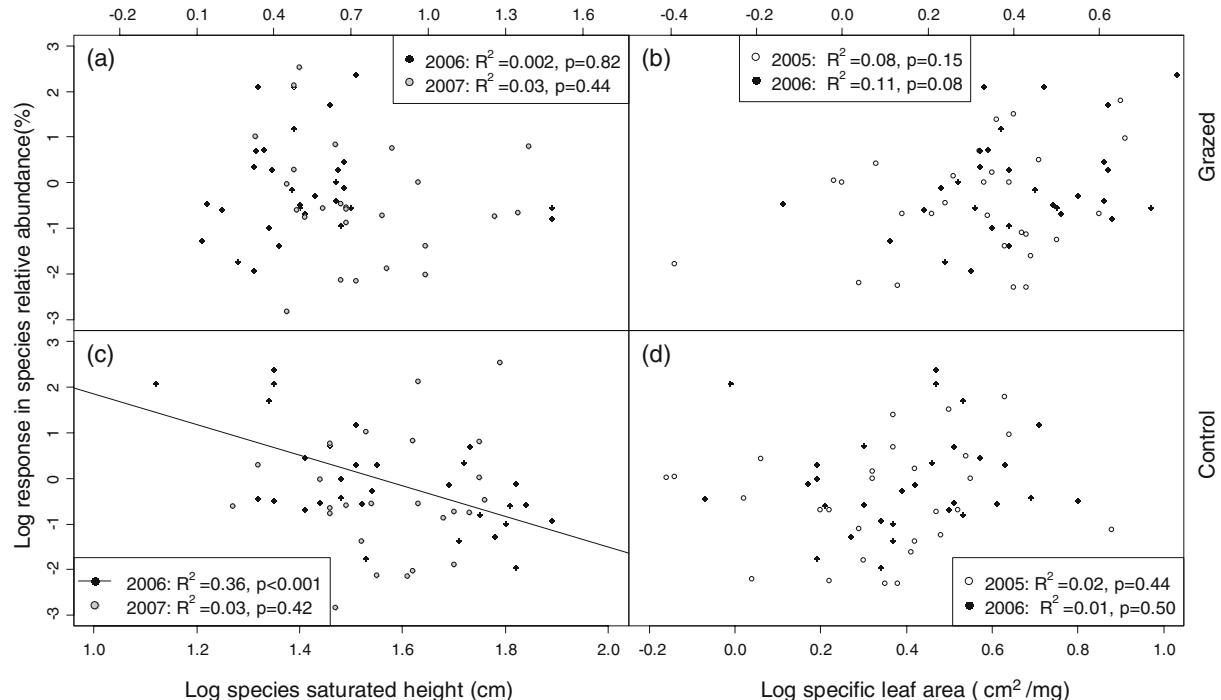
**Fig. 1** Effect of grazing on species abundance (a), specific leaf area (b) and species saturated height (c) over 3 years. The means and standard error of the log response ratio of species relative abundance and functional traits in grazed (G) or control (C) communities are shown with graminoids contrasted with

forbs (NS or different letter above the bar indicates the non-significant or the significant effect of grazing on species abundance or functional traits, respectively, or the difference between graminoids and forbs,  $p < 0.05$ , tested by  $t$ -test). See “Material and methods” for details

strategy (Bazzaz et al. 1987; Stearns 1992; Gibson 2009). This specific response in functional traits is often proposed as the main driver for the response of species abundance at population and community levels (Tilman 1988; Bazzaz 1996; Grime 2001).

Can the response of species abundance be predicted by plant functional traits?

Plant functional traits provide one tool for predicting the effects of grazing on species abundance and



**Fig. 2** The relationship between the response of species abundance and species saturated height (a and c) and specific leaf area (b and d) in the grazed (a and b) and control (c and

d) community over 3 years.  $R^2$  and  $p$  value was estimated from a linear regression model. See “Material and methods” for details

community structure. Our results indicated that there are some weak correlations in the response directions of species abundance and functional traits. Tall species tended to decrease in their abundance response to grazing (Fig. 2c). This trend has been repeatedly predicted in theory and has been observed in previous studies (Westoby et al. 1999; McIntyre and Lavorel 2001; Vesk and Westoby 2001; Diaz et al. 2007). Moreover, we found that the extent of the grazing response of species relative abundance can partly be explained by the species saturated height, although the linear relationship was significant only in the control community of 2006 (Fig. 2b), suggesting that plant Hs are a better predictor of species abundance in control communities than in grazed communities. Thus it could be inferred that taller species tend to suffer more seriously from grazing pressure and declines in their relative abundance than shorter species. It could be that short species benefit from avoiding leaf loss through relaxed competition. Similar to this study, Diaz et al. (2001) found that plant life form and Hs are powerful predictors for grazing response (Diaz et al. 2001, 2007).

However, we did not find any significant correlation between response extent of species abundance and SLA or seed size in either grazed or control communities over the 3 years. The combination of SLA and SS with Hs did not improve the predictability of Hs to response of species abundance to moderate grazing. This was a challenge to the prediction that under moderate grazing intensity, plants with larger SLA are often favored under grazing (Westoby et al. 1999; Wilson et al. 1999; Cingolani et al. 2005; Diaz et al. 2007). This was supported by our observation that the yaks and sheep prefer more palatable species such as *Kobresia* with smaller SLA than the relatively unpalatable species such as *Elymus* or *Roegneria* with a larger SLA (unpublished data). In fact, in perennial herbaceous plant dominated Tibetan alpine meadows, most species with larger SLA such as Ranunculaceae and Compositae are forbs which are not grazed by yaks or sheep. Plants with small SLA such as *Kobresia* sp. often belong to Cyperaceae or Poaceae which is preferred by grazers under moderate grazing intensity.

Overall, our study of alpine perennial meadow indicated that the direction of grazing response in species abundance can be predicted by functional

traits. However, the predictability of the extent of grazing response in species abundance from functional traits is very weak which is consistent with a previous study (Vesk et al. 2004). Many causes may contribute to this pattern, for example when several functional traits or combinations of a small number of traits can not adequately capture the ecological strategy of a species, the grazing effect and plant response is more complicated because the effect and response may be delayed in perennial herbaceous dominated Tibetan alpine meadows with very short season. This is consistent on the some meta-analysis of grazing response (Pakeman 2004; Diaz et al. 2007). Furthermore, in linking functional traits to grazing response of species abundance, it was unclear which functional traits in which habitat are more reasonable. We believe further empirical studies are needed to understand the response of functional traits to grazing and its role in the dynamic of population and vegetative processes in different situations.

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