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Community-weighted mean traits but not functional diversity determine the changes of soil properties during wetland drying on the Tibetan Plateau

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Running Title: Community-weighted mean traits determines soil properties

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Abstract. Climate change and human activities have caused a shift in vegetation composition and soil biogeochemical cycles of alpine wetlands on the Tibetan Plateau. The primary goal of this study was to test for associations between community-weighted mean (CWM) trait and functional diversity, and soil properties during wetland drying. We collected soil samples and investigated the above-ground vegetation in swamp, swamp meadow and typical meadow; four CWM trait values (specific leaf area, SLA; leaf dry matter content, LDMC; leaf area, LA; and mature plant height, MPH) for 42 common species were measured across the three habitats; three components of functional diversity (functional richness; functional evenness; and functional divergence) were also quantified in these sites. Our results showed that the drying of the wetland dramatically altered plant community and soil properties. There was a significant correlation between CWM of traits and soil properties, but not a significant correlation between functional diversity and soil properties. Our results further showed that CWM-LA, CWM-SLA and CWM-LDMC had positive correlations with soil readily available nutrients (available nitrogen, AN; available phosphorus, AP), but negative correlations with total soil nutrients (soil organic carbon, SOC; total nitrogen TN; and total phosphorus, TP). Our study demonstrated that simple, quantitative plant functional traits, but not functional diversity, are directly related to soil C/N properties, and likely play an important role in plant-soil interactions, and our results also suggest that functional identity of species may be more important than functional diversity in influencing ecosystem processes during wetland drying.

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1 Introduction

About one third of China's natural wetlands are situated on the Tibetan Plateau, according to a state-of-the-art remote sensing-based classification (Gong et al., 2010). The wetlands of Maqu on the Tibetan Plateau are one of the highest wetlands, and they play very important role in water resources conservation, and in regulating the river systems and regional climates across the entire Yellow River basin (Cai and Guo 2007). However, these wetlands are also climate-sensitive and have been gradually shrinking and drying due to climate change and human activities, such as heavy grazing and land use changes (Cai and Guo 2007; Peng et al., 2015; Wang et al., 2016). Hence, it is imperative that we examine the changes of vegetation and soil, and the relationships between them during this process of wetland drying for prediction and conservation efforts.

Previous studies have suggested that there may be a secondary successional change from swamp to swamp meadow and mature meadow, and that soil water availability may be the main driver of this succession process (Ma et al., 2014; He and Richards, 2015; Lin et al., 2015). At the same time, plant functional traits play an important role in predicting the patterns of species composition, community structure, and their responses to environment change, which has drawn substantial ecological interest (e.g., Wright et al., 2004; McGill et al., 2006; Pérez et al., 2014; Li et al., 2015); but it is not clear whether functional traits and functional diversity (i.e., the identity, abundance and range of species in a given community) can reflect the changes of soil properties during wetland drying on the Tibetan Plateau. A growing body of evidence has shown that functional diversity is directly linked with ecosystem processes (McGill et al., 2006; Flynn et al., 2011). However, recent studies have shown that environmental disturbance (e.g., fertilization or grazing) did not influence the value of functional diversity (Li et al., 2015; Niu et al., 2015), and functional traits of species may be more important than functional diversity in influencing ecosystem processes in an alpine meadow community (Li et al., 2015).

As the relationships between the plant community and environmental factors are dynamic, certain traits may be used to predict the changes of environmental factors

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(Lavorel and Garnier, 2002; Suding et al., 2008). At the species scale, some leaf traits that respond to water or nutrient availability (e.g. leaf dry matter content (LDMC) and leaf nitrogen content (LNC)) also affect leaf palatability and litter decomposability (Diaz et al., 2004). Similar to this, at the community scale, the community-level means of some functional traits (e.g. specific leaf area (SLA), leaf area (LA), LDMC or plant height) weighted by their relative abundances can respond to environmental change in grasslands, and affect nutrient cycling and dynamics (Garnier et al., 2004; Quétier et al., 2007).

The "mass ratio hypothesis" proposed by Grime (1998) implies that the functioning of ecosystems is determined to a large extent by the trait values of the dominant species. This hypothesis was confirmed by some studies that account for ecosystem functions such as primary productivity (Garnier et al., 2004) and nitrification (Laughlin, 2011). Conversely, the "diversity hypothesis" postulates that the traits diversity within a community can affect ecosystem processes (Tilman, 1997). The high functional diversity may allow for a more complete use of resources among species, thereby improving biomass production and nutrient cycling in ecosystems (Loreau, 2000; Díaz and Cabido, 2001; Villéger et al., 2008; Mouchet et al., 2010).

The plant functional traits selected therefore pertain to the processing of resources at the species level, with the underlying assumption that this would scale up to ecosystem functioning (Lavorel and Garnier, 2002). We chose four functional traits, known to affect nutrient cycles at the leaf, whole-plant, and ecosystem levels (Cornelissen et al., 1999; Lavorel and Garnier, 2002): specific leaf area (SLA, the ratio of water-saturated leaf area to leaf dry mass), leaf dry matter content (LDMC, the ratio of leaf dry mass to water-saturated fresh mass), leaf area (LA) and mature plant height (MPH). SLA is an important variable in comparative plant ecology because it is closely related with relative growth rate (Wright et al., 2001) and leaf net assimilation rate (Shipley and Lechowicz, 2000); it is also a good predictor of plant response to resource availability (Grime, 1977). LDMC is tied to plant nutrient retention and water (Poorter and Garnier, 1999). LA has important consequence for the leaf energy and water balance (Cornelissen et al., 2003). MPH has been associated

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with competitive ability in herbaceous plant communities, with the general idea that light competition becomes more intense at high soil fertility when above-ground biomass or vegetation stature increases (Hautier et al., 2009). Fast growing species from nutrient-rich habitats usually have high SLA, high LNC and low LDMC, while opposite trends characterize species from nutrient-poor habitats (Diaz et al., 2004). These responses reflect a fundamental trade-off (leaf economics spectrum) between traits related to nutrient conservation and traits related to nutrient acquisition and turnover (Wright et al., 2004).

In this study, we investigate whether soil properties are affected by plant functional traits and functional diversity during wetland drying. Ongoing extensification of human activities has affected the functional composition and structure of wetlands on the Tibetan Plateau (Cai and Guo, 2007; Peng et al., 2015). At the same time, the soil nutrient availability has also been modified (Robson et al., 2007), and this has been directly linked to community-level trait changes in response to environmental dynamics (Diaz et al., 2007). The aim of this study was to answer the following questions: (1) How do community composition and structure, and soil nutrient characteristics, change following wetland drying on the Tibetan Plateau? (2) Can the community weighted mean (CWM) trait values and functional diversity be regarded as predictors of soil properties during wetland drying?

2 Materials and methods

2.1 Study site

This study was conducted at the Research Station of Alpine Meadow and Wetland Ecosystems of Lanzhou University (N 33°58′, E101°53′) (Fig. 1). The site is located on the eastern Tibetan Plateau. The mean annual temperature is 1.2 ℃, ranging from -10 ℃ in January to 11.7 ℃ in July, and the mean annual precipitation (calculated from 1975 to 2010) was 620 mm, occurring mainly during the short, cool summer (Li et al., 2011). The annual duration of cloud-free solar radiation is about 2580 h, and there are on average 270 frost days per year. The soil type of the study area is alpine meadow soil. Parent materials are from a variety of glacial deposits, alluvial deposits, residual deposits, residual slope deposits, etc. (Chen and Wang, 1999). The

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149 experiment was carried out in typical mature meadow, swamp meadow and swamp
150 which are adjacent to each other in our study area. These habitats have different
151 community compositions, structures and dominant species (Table 1).

152 **2.2 Experimental design and community measurements**

153 Twenty five sampling plots (10 m × 8 m) were selected in each meadow type.
154 Each plot was separated from the others by a 2-m buffer strip. Each plot was
155 separated into two subplots: a 4m × 8 m subplot for community investigation and soil
156 collection, and a 6 m × 8 m subplot for individual plant sampling. Community
157 measurements were conducted from 5 to 8 Sept 2010. One 0.25 m^2 quadrat was
158 harvested from the 4 m × 8 m subplot in each plot. The quadrat location was randomly
159 selected with the constraint that it was at least 0.5 m from the margin to avoid edge
160 effects. We estimated the cover of each species and vegetation before it was clipped
161 and brought to the lab. For clonal species, an individual plant was defined as a group
162 of tillers connected by a crown (Luo et al., 2006). The cover of each species in each
163 plot was estimated as a percentage using a canopy interception technique based on
164 cardboard cut-outs of various shapes and sizes as visual guides. All samples were
165 dried at 80 °C for 48 h, and weighed to the nearest 0.01 g. Above-ground biomass was
166 calculated by summing all dried biomass of harvested individuals within a quadrat.

167 **2.3 Soil collection and processing**

168 Soil samples (0–15 cm depth) were collected from each quadrat in each sampling
169 plot of each habitat, after the above-ground material was harvested. In each quadrat,
170 soil was randomly collected from three points (3.8 cm in diameter) using a bucket
171 auger and mixed into a single soil sample. All of the soil samples were brought into
172 the laboratory in airtight plastic bags. All of the soil samples were air-dried and then
173 filtered through a 0.2-mm sieve, discarding the visible roots and other plant debris.
174 Soil pH was measured using a pH meter with a glass electrode (soil/KCl ratio 1:2.5).
175 Soil water content was obtained by the oven-drying method. Soil organic carbon was
176 determined by wet oxidation with potassium dichromate ($K_2Cr_2O_7$), both dichromate
177 oxidation and dry combustion, using a carbon analyser with the Mebius method for
178 the Walkley-Black acid digestion (Kalembasa and Jenkinson, 1973). The soil total

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nitrogen, available nitrogen, total phosphorus and available phosphorus were measured by the methods of Miller and Keeney (1982).

Plant functional trait measurements

Following Perez-Harguindeguy et al. (2013), we measured four functional traits (SLA, LDMC, LA and MPH) of 42 common species for three habitats in early September 2010. These species represented 85-95% of the peak standing biomass and 80–90% of the vegetation cover of the total plant community in the studied plots. We randomly sampled 1 individuals and 3 mature leaves at flowering time for each of the 42 species in each 6m × 8 m subplot. That is, 25 individuals and 75 mature leaves were measured for each of the 42 species in each habitat. Mature plant height is the shortest distance between the upper foliage boundary and ground level. Leaves were scanned to measure leaf area in the field, and fresh weight of leaves was determined with a balance (Acculab Lt-320; Acculab, Measurement Standards Inc., Danvers, MA, USA). Following these measurements, leaves were placed in paper bags and dried in the sun. Leaf samples were oven-dried at 80 °C for 48 h in the laboratory, and their dry masses were measured on a semianalytical balance with an accuracy of 10^{-4} g (Sartorius AG, Goettingen, Germany).

2.4 Statistical analysis

From the vegetation harvest data, we calculated the species richness (Pielou, 1969) represented by the number of species recorded in each quadrat. Following Garnier et al. (2004), the community-weighted mean (CWM) trait values for each trait were calculated for every sample using species mean trait values and species relative cover: $CWM = \sum_{i=1}^{S} P_i \times trait_i$, and $trait_i$ is the trait value of species i.

Although various indices have been proposed to measure the functional diversity of a community, there is still no consensus on which are most suitable. Villéger et al. (2008) suggested that some of functional diversity are redundant and they recommended using three independent components of functional diversity - functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv). In this study, we chose FRic, FEve and FDiv to examine how different components of functional diversity responded to different habitat types. We used the FDiversity

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software program to calculate FRic, FEve and FDiv after the traits were standardized to ensure equal contribution of each trait.

We used one-way ANOVA to test the effect of different habitat types on plant taxonomic diversity (species richness), the CWM traits, functional diversity (FRic, FEve and FDiv) and soil properties. Correlations between the CWM traits and soil properties were tested using Pearson correlation coefficients, and a principal component analysis (PCA) on standardized data was conducted to analyze the overall pattern of correlations between soil properties, functional diversity and aggregated trait values. These statistical analyses were performed using the R 3.2.3 software (R Development Core Team, 2011).

3 Results and Analysis

3.1 Vegetation response

Wetland drying had obvious effects on vegetation composition and structure, and our study demonstrated that the species richness, vegetation cover and above-ground biomass significantly increased with wetland drying (Table 1). Species richness increased approximately 120.8% from swamp meadow to typical meadow relative to swamp (Table 1). Vegetation cover increased approximately 10.7% in swamp meadow and typical meadow relative to swamp (Table 1). Above-ground biomass increased approximately 36.3% in swamp meadow and typical meadow relative to swamp (Table 1). There was also significant difference in species composition among the community types (Table 1). Many typical wetland plants gradually disappeared from the vegetation after wetland drying occurred; these included *Carex meyeriana, Blysmus sinocompressus, Rumex patientia, Nardostachys jatamansi, Caltha palustris, Sanguisorba filiformis, and Cremanthodium lineare.* Others greatly decreased in abundance, mainly *Deschampsia caespitosa*. Meanwhile, many other new species emerged from the typical meadow, such as *Kobresia capilifolia, Poa poophagorum, Festuca ovina, and Anemone rivularis*, all adapted to a high drought environment.

3.2 Community-weighted means of traits and functional diversity response

Community-weighted means of traits differed greatly between the three habitats. The CWM-LA, CWM-SLA and CWM-LDMC significantly increased with the

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wetland drying (Fig.2a ,b, and c), however, the CWM-MPH of swamp (Fig2d) was significantly higher than the swamp meadow and typical meadow. Functional richness (Fig.3a), functional evenness (Fig.3b) and functional divergence (Fig.3c) had not obvious changes with the wetland drying. These results also further showed that community-level traits responses (community-weighted means of traits and functional diversity) were totally different, and the single-trait level responses may be more sensitive than multi-trait level responses in the process of wetland drying.

3.3 Soil response

Wetland drying had obviously different effects on different soil characteristics. Soil organic carbon (SOC) (Fig. 4a), soil total nitrogen (TN) (Fig. 4b), soil total phosphorus (TP) (Fig. 4c), and soil moisture (SM) (Fig. 4f) of the swamp were significantly higher than the swamp meadow and the typical meadow. However, soil available nitrogen (AN) (Fig 4d), soil available phosphorus (AP) (Fig. 4e) and soil pH (Fig. 4g) of the swamp were significantly lower than that of the swamp meadow and the typical meadow. These results clearly demonstrated that the changes of soil readily available nutrients (AN and AP) and total soil nutrients (SOC, TP and TP) may be habitat-dependent and the soil water content may be the first driving factor with the wetland drying.

3.4 Relationships between CWM traits, functional diversity and soil properties

Simple correlations and a PCA combining data on soil properties, community functional diversity and the community-weighted means of traits (CWM) were conducted. The analyses revealed a significant correlation between soil properties and CWM of traits, but not a significant correlation between soil properties and functional diversity (Table 2). Fig. 5 further shows that there was a significantly positive correlation between SOC, TN, TP, and SM and CWM-MPH, but a significantly negative correlation between AN, AP, and pH and CWM-MPH (Table 2, Fig. 5). In contrast, there was a significantly negative correlation between SOC, TN, TP, and SM and CWM-SLA, CWM-LDMC and CWM-LA, but a significantly positive correlation between AN, AP, pH and CWM-SLA, CWM-LDMC and CWM-LA (Table 2, Fig. 5). In addition, the functional richness (FRic) had a positive relationship with functional

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divergence (FDiv), but negative relationship with functional evenness (FEve) (Fig. 5). Thus, these results showed that community responses of single-functional trait level may play crucial role in influencing soil properties during wetland drying.

4 Discussions

4.1 Responses of above-ground community composition and functional traits

Our study demonstrated that the species richness, vegetation cover and above-ground biomass significantly increased with wetland drying, and there was also significant difference in species composition among the community types. Many typical wetland plants disappeared from the community after wetland drying occurred, and many other new species (adapted to a high drought environment) emerged from the typical meadow.

Previous studies have shown that SLA and LA are often closely positively correlated with photosynthesis and transpiration rate (Reich et al., 1999; Westoby et al., 2002), and plants with an exploitative strategy (e.g. high SLA and transpiration rate) are often drought intolerant (Reich et al., 1999; Diaz et al., 2004). Our results also demonstrated that some forbs species (e.g. *C. palustris, N. jatamansi,* and *R. patientia*; usually with higher SLA and LA) dominated in the swamp meadow. These forbs species tended to deplete soil moisture more quickly than grass species, therefore further aggravating the trend of drying of the entire community. Following this, some grass species (e.g. *E. nutans, P. poophagorum*, and *K. cristata*) with high LDMC would dominate in the typical meadow. Although forb species account for less total biomass than the grass species, they formed the bulk of the species diversity in this community, as in most herbaceous communities (Grime, 1998). Plant height has been associated with competitive ability for light interception in herbaceous plant communities, with the general idea that light competition becomes more intense when above-ground biomass or vegetation stature increases (Hautier et al., 2009). In the present study, our results showed that taller plants dominated (e.g., *D. caespitosa*) in the swamp, due to accumulated standing water in summer, but shorter plants dominated in the swamp meadow and typical meadow due to light not being a limiting factor in these communities.

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299 In contrast, the functional diversity (FRic, FEve, and FDiv) (Fig. 3a ,b, and c)
300 did not show any significant change among the three habitats (Fig. 3). We speculated
301 that these changes in functional diversity would primarily be determined by the
302 balance between competitive exclusion and stabilizing niche differences (Chesson,
303 2000; Hille Ris Lambers et al., 2012). First of all, functional diversity may decrease
304 when stabilizing niche differences are smaller than is needed to overcome competitive
305 exclusion. Second, functional diversity may increase when stabilizing niche
306 differences of species are greater than competitive exclusion. In addition, the
307 responses of functional diversity can be constrained by close functional linkages to
308 any number of traits determining performance at the whole plant level (Reich, 2014).
309 Trade-offs in the responses within a suite of traits can create approximately equal
310 performance at the whole plant level and hence a low value for change in functional
311 diversity (Shiply et al., 2006). These results are consistent with many recent
312 observations that the response of functional diversity to fertilization and grazing is
313 relative stable (Niu et al., 2015; Li et al., 2015) and highlights the potential
314 complexity of community responses to environmental change.

315 **4.2 Response of below-ground soil properties**

316 Our results showed that the soil of the swamp had significantly higher moisture,
317 organic carbon, total phosphorus, and total nitrogen, but lower pH, available nitrogen,
318 and available phosphorus than the swamp meadow and typical meadow. These results
319 indicates that the soil total nutrient content had a decreasing trend with wetland drying.
320 The wetlands can accumulate a large amount of soil organic matter because of lower
321 decomposition rates of litter, due to permanent or temporary anaerobiosis associated
322 with waterlogged conditions (Nieder and Benbi, 2008). However, the drying of
323 wetlands can stimulate microbial activity and increase mineralization of soil organic
324 matter (Denef et al., 2001), therefore leading to an increase of soil readily available
325 nutrients, such as nitrogen, and phosphorus. However, other studies have reported that
326 a reduction in mineralization with drying could be caused by reduced microbial
327 activity and mobility (Pulleman and Tietema, 1999). In swamp meadow and typical
328 meadow, certain factors can contribute to reduced soil total nutrient content. First,

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329 trampling by livestock (yak and Tibetan sheep) can lead to compaction and changes in
330 infiltration rates, bulk density, and decline of edaphon activity (Li et al., 2011;Yu and
331 Jia, 2014); Second, under the long-term pressure of grazing, some energy and
332 nutrients are transferred to livestock (Li et al., 2011; Lu et al. 2015). In addition, the
333 available forms of nitrogen and phosphorus in the wetland are lower than in the
334 typical meadow, because they are very water-soluble and move rapidly in the wetland
335 environment.

336 **4.3 Relationships between CWM traits, functional diversity and soil properties**

337 Simple correlations and a PCA analyses strongly support the idea that
338 fast-growing plant species can promote the rates of soil C, N and P cycling, which in
339 turn results in high nutrient availability, but relatively low C and N sequestration. A
340 striking result of the present study is that above-ground plant traits can determine the
341 changes of below-ground soil properties during wetland drying. There are two likely
342 reasons to explain this phenomenon. First, it is possible that high-quality litter results
343 in high decomposition rates in suitable environmental conditions, whereas
344 lower-quality litter might result in a more consistent level of microbial activity due to
345 the longer residence time of the litter in soil. For the swamp, the accumulation of SOC,
346 TN, and TP was greater than in swamp meadow and typical meadow, because primary
347 production exceeds the slow mineralization rates, caused by permanent or temporary
348 anaerobiosis associated with waterlogged conditions (Nieder and Benbi, 2008).
349 Second, other factors that co-varied with leaf and litter quality may have been more
350 important drivers of soil properties. For example, the results of our study support that
351 greater litter diversity associated with species diversity (in typical meadow) can
352 stimulate a large and active soil microbial community, which further results in higher
353 rates of litter decomposition and higher soil nutrient availability (Wardle et al., 2006).
354 In addition, in this study, fast growing species (with higher SLA and LA) that produce
355 high-quality litter may exceed slow-growing species (with higher LDMC) which
356 produce a litter of lower quality, therefore remained the higher rates of litter
357 decomposition in swamp meadow and typical meadow. Some models study such as
358 BIOME-BGC (Running and Hunt, 1993) or CENTURY (Parton et al., 1993) also

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suggest that some key functional traits, such as SLA, LDMC, LA and MPH, can directly affect ecosystem properties. Additionally, positive effects of plant functional traits on soil properties may also result in positive or negative feedback effects, which influence plant community dynamics and composition (McLaren, 2006). In this study, higher soil available nutrients changed plant community structure and productivity to favor graminoid species, which have greater competitive and colonization abilities (e.g. *K. capilifolia, E. nutans, P. poophagorum*) over forb species in typical meadow (Moretto & Distel 1997; Van der Wal et al., 2004; Li et al., 2015).

Our results showed that functional diversity had no measurable effect on soil properties. Many studies have found that functional diversity does not influence litter decomposition and nutrient cycling (Barantal et al., 2011; Schindler and Gessner, 2009). However, these studies typically use only one metric of functional diversity. Functional diversity is complex, and single metrics may not capture its effects (Mason et al., 2005). In this study, we used three metrics of functional diversity (FRic, FEve and FDiv), yet we still did not find evidence for a relationship between functional diversity and soil properties. We found little evidence to support the diversity hypothesis, which predicted that trait diversity would perform better in litter mixtures because those mixtures would better provision the variety of nutrients that plants need. These results also suggested functional diversity (traits taken in aggregate) may not directly related to with ecosystem functioning (Li et al., 2015). Zuo et al. (2016) directly measured the relationship between plant functional traits and the C and N storage in plant, litter, root, and soil along a restoration gradient of sandy grassland in northern China, and their results showed that ecosystem C and N pools are primarily associated with the traits of the most abundant species in communities, thereby also supporting the biomass ratio hypothesis. Overall, these results suggest soil properties are likely to be predictable based on plant functional traits and/or litter quality, but not functional diversity. However, predicting soil properties from plant functional traits is likely to be a complex process.

5 Conclusions

Our study has demonstrated that simple, quantitative plant functional traits, but

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not functional diversity, could provide relevant information on key aspects of ecosystem functioning. We have also shown that the particular traits selected here, specific leaf area, leaf dry matter content, leaf area, and mature plant height could be used to capture the functioning of plant species and communities. Our observations also promote a better understanding of plant–soil feedbacks for plant functional traits in plant communities, but long-term monitoring is needed, especially in different times of the year in future research, because the cycling and sequestration of soil nutrients may be "fast-out, slow-in" processes with high variation due to regulation by environmental factors (Schulze, 2006).

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628 Table 1 Brief descriptions for vegetation properties (species richness, vegetation cover, above-ground biomass, and dominant species), grazing
629 intensity and standing water status during the wetland drying. S, swamp; SM, swamp meadow; TM, typical meadow. Significant differences
630 across treatments within each variable were determined using Tukey's Honest Significant Difference test ($P < 0.05$) after one-way analysis of
631 variance and are indicated by dissimilar letters.

Types	Species richness (no. 0.25m^{-2})	Vegetation cover (%)	Above-ground biomass (g 0.25m^{-2})	Dominant species	Grazing intensity	Standing water status
S	7.9(1.85)c	72.3%(13.12%)b	56.9(10.84)c	*Deschampsia caespitosa, Carex meyeriana, Blysmns sinocompressus, Nardostachys jatamansi, Caltha palustris*	Lightly grazed by livestock (yak and Tibetan sheep).	It was dry for most of the whole year, with about four months (July to October) having standing water during the rainy season.
SM	14.2(1.98)b	71.3%(9.23%)b	97.6(8.66)b	*Nardostachys jatamansi, Deschampsia caespitosa, Caltha palustris, Rumex patientia, Sanguisorba filiformis, Cremanthodium lineare*	Grazing disturbance by Tibetan sheep and yak was higher than that in swamp.	No standing water at any time for the whole year.
TM	20.7(1.77)a	88.5%(12.17%)a	124.4(11.27)a	*Kobresia capilifolia, Elymus nutans, Poa poophagorum, Koeleria cristata, Anemone rivularis, Trollius farreri, Festuca ovina*	Grazing disturbance was similar with swamp meadow.	No standing water at any time for the whole year.

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632 Table 2 Relationships between CWM trait and soil properties from a Pearson's correlation analysis.

	Soil organic carbon (g kg^{-1})	Soil total nitrogen (g kg^{-1})	Soil total phosphorus (g kg^{-1})	Soil available nitrogen (mg kg^{-1})	Soil available phosphorus (mg kg^{-1})	Soil moisture (%)	Soil pH value
CWM-SLA (cm^2 g^{-1})	-0.805**	-0.781**	-0.364*	0.485*	0.730**	-0.844**	0.733**
CWM-LDMC (g g^{-1})	-0.803**	-0.735**	-0.778**	0.764**	0.771**	-0.815**	0.748**
CWM-LA (cm^2)	-0.428*	-0.602**	-0.312*	0.628**	0.624**	-0.710**	0.696**
CWM-MPH (cm)	0.573*	0.453*	0.464**	-0.395*	-0.538**	0.530**	-0.494*
Functional richness	-0.331	-0.274	-0.321	0.216	0.187	-0.377	0.038
Functional evenness	-0.272	-0.283	-0.367	0.239	0.221	-0.339	0.201
Functional divergence	-0.318	-0.248	-0.379	0.313	0.312	-0.299	0.04

633 Notes: CWM, community-weighted mean trait values; SLA, leaf area per unit dry mass; LDMC, leaf dry matter content; LA, leaf area; MPH,
634 mature plant height. *, $p<0.05$; **, $p<0.01$.

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635 **Figure legends**

636 **Fig. 1** The location of the Tibetan Plateau in China and our study site (the Research
637 Station of Alpine Meadow and Wetland Ecosystems of Lanzhou University) at the
638 Tibetan Plateau..

639 **Fig. 2** The changes of CWM trait across three habitats. CWM, community-weighted
640 mean trait values; SLA, leaf area per unit dry mass; LDMC, leaf dry matter content;
641 LA, leaf area; MPH, mature plant height; S, swamp; SM, swamp meadow; TM,
642 typical meadow; Significant differences indicated by dissimilar letters above each bar
643 were determined using Tukey's honestly significant difference (HSD) test ($P< 0.05$)
644 after one-way ANOVA.

645 **Fig. 3** The changes of functional diversity (functional richness, functional evenness,
646 and functional divergence) across three habitats. Significant differences indicated by
647 dissimilar letters above each bar were determined using Tukey's honestly significant
648 difference (HSD) test ($P< 0.05$) after one-way ANOVA.

649 **Fig. 4** The changes of soil properties across three habitats. S, swamp; SM, swamp
650 meadow; TM, typical meadow; Significant differences indicated by dissimilar letters
651 above each bar were determined using Tukey's honestly significant difference (HSD)
652 test ($P< 0.05$) after one-way ANOVA.

653 **Fig. 5** Principal components analysis combining data on soil properties, CWM trait
654 and functional diversity. Only the first two axes (PC1 and PC2), which account for
655 80% of the total variation, are retained here. The first axis, which can account for 71%
656 of the total inertia, and it differentiates communities according to soil moisture: the
657 communities of higher soil moisture showed higher SOC, TN, TP and CWM-MPH
658 while the communities of lower soil moisture showed higher AN, AP, pH, CWM-LA,
659 CWM-SLA and CWM-LDMC. The second axis, which can account for 9% of the
660 total inertia, and it showed that functional richness (FRic) had a positive relationship
661 with functional divergence (FDiv), but negative relationship with functional evenness
662 (FEve).

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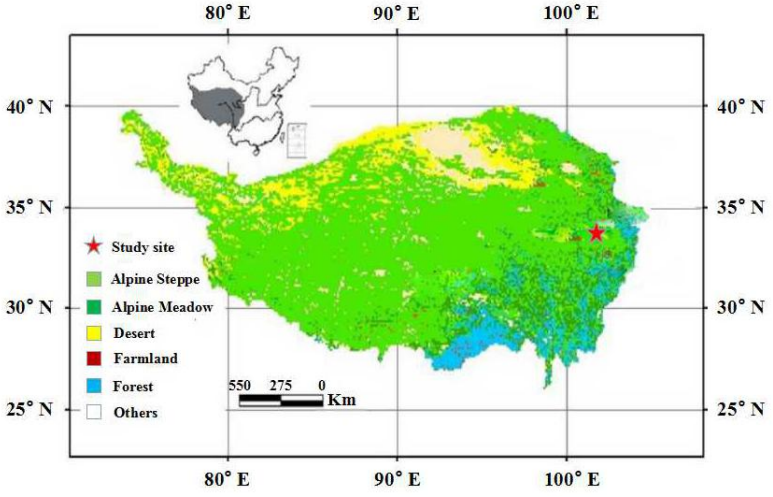

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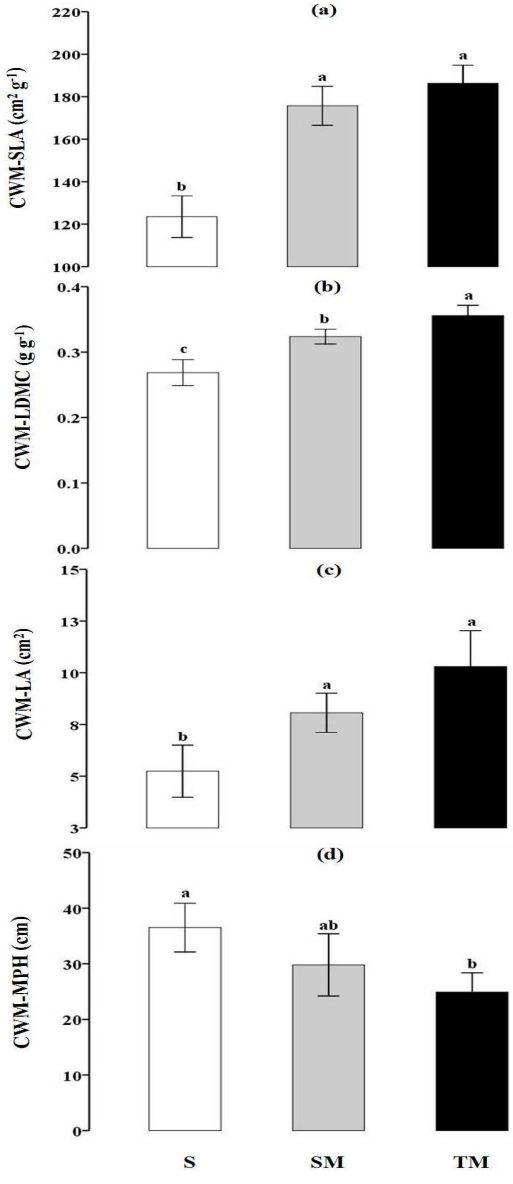

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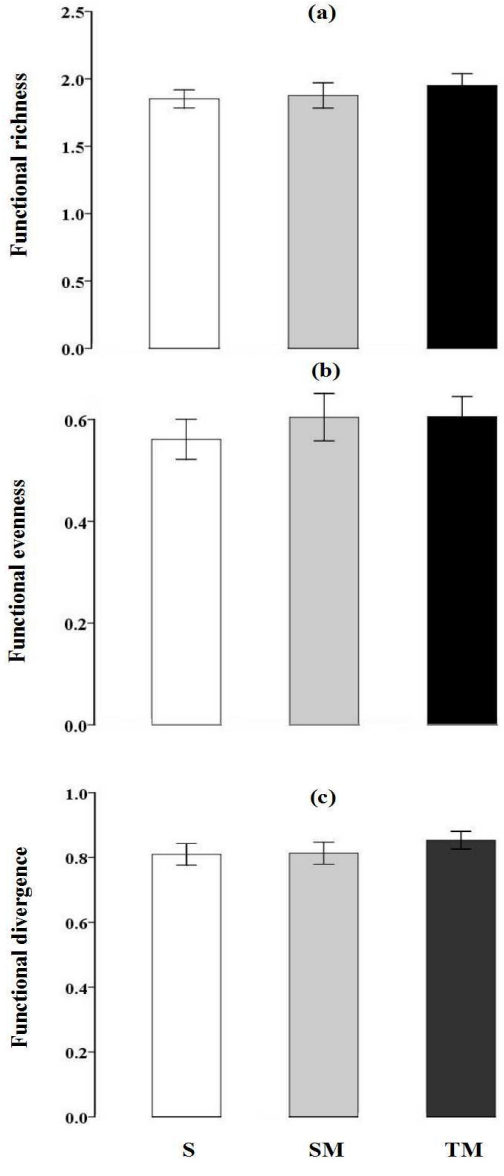

Fig. 3 The changes of functional diversity (functional richness, functional evenness, and functional divergence) across three habitats. Significant differences indicated by dissimilar letters above each bar were determined using Tukey's honestly significant difference (HSD) test ($P < 0.05$) after one-way ANOVA.

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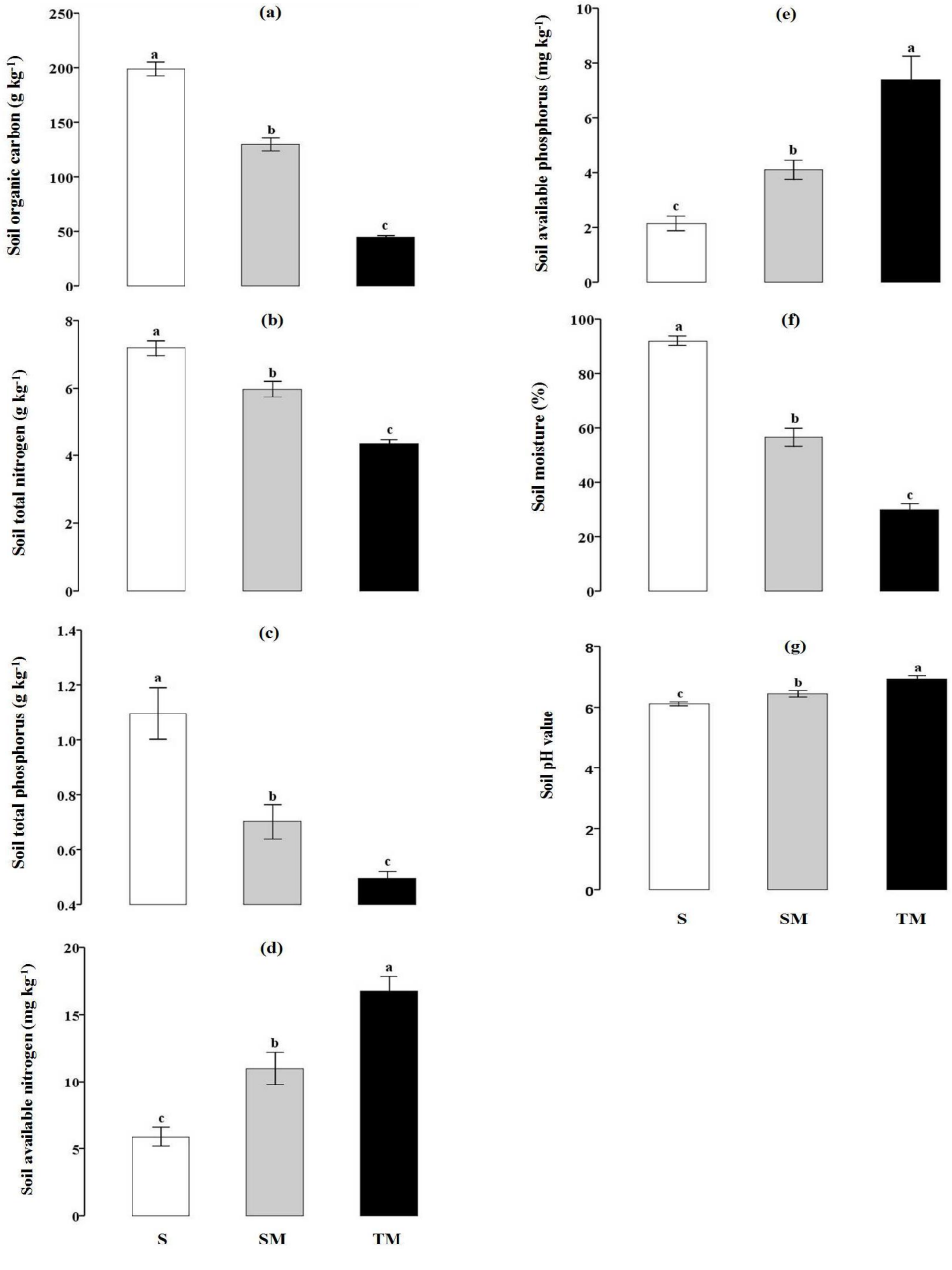

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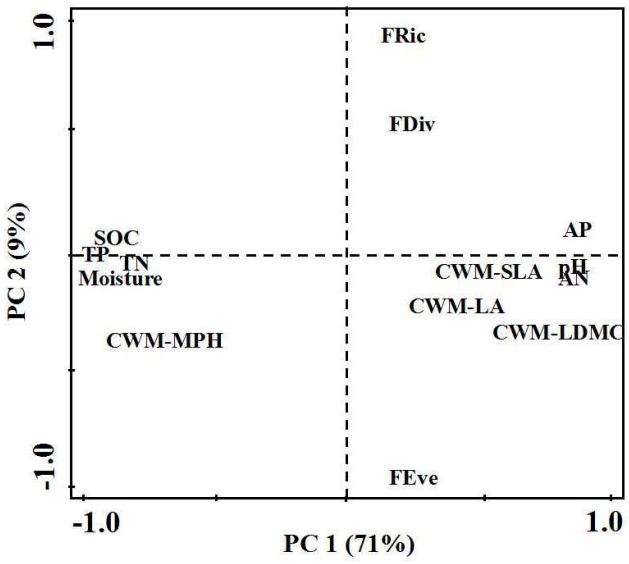

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