Journal of
Plant Ecology

Research Article

Effects of the hummock–depression microhabitat on plant communities of alpine marshy meadows in the Yellow River Source Zone, China

Guiling Wu[1,2], Jay Gao[3], Weiyou Ou[4], Jizhong Wan[1] and Xilai Li[1,2,*]

[1]State Key Laboratory of Plateau Ecology and Agriculture, Qinghai University, Xining 810016, China, [2]College of Agriculture and Animal Husbandry, Qinghai University, Xining 810016, China, [3]School of Environment, University of Auckland, Private Bag 92019, Auckland, New Zealand, [4]Qinghai Provincial Grassland Station, Xining 810016, China

*Corresponding author. E-mail: xilai-li@163.com

Handling Editor: Christian Schöb

Received: 11 September 2020, **First Decision:** 2 December 2020, **Accepted:** 6 June 2021, **Online Publication:** 14 July 2021

Abstract

Our objectives are to examine the effects of hummock–depression spatial heterogeneity on plant communities and soil properties, and to understand the process of maintaining and adjusting microtopography-mediated hydrological inputs and their spatial fluctuations that produce obvious microhabitats. We set up 36 plots (1 m × 1 m) and sampled 45 plant and 225 soil samples in flooded (FH) and non-flooded hummocks (NFH) and depressions of the marshy, and the surrounding non-wetland meadows as well as in the Yellow River Source Zone, west China. We evaluated whether the alpine marshy wetland has a fertile island effect by the comparison method. Our results show that hummock presence can increase the spatial heterogeneity of the microhabitat and promote the plant diversity and soil fertility of the *Kobresia tibetica* community. Plant height, coverage, above-ground biomass, species richness and diversity were significantly higher in the FH and NFH microhabitat than in the areas between hummocks and surrounding non-wetland meadows. Compared with broad alpine meadows, the hummock–depression complex provided a microhabitat favorable to the growth of Cyperaceae. In the 0–50 cm soil layer, the closer the soil layer was to the ground surface, the higher its soil organic carbon and total nitrogen contents. Thus, in deeper layers, the gap between soil nutrients in wetland hummock–depression microhabitat and in the surrounding alpine meadows becomes smaller. Hence, the wetland hummock–depression microhabitat formed a fertile island pattern. Therefore, these results contribute toward improving our understanding of ecosystem restoration in alpine marshy meadows.

Keywords alpine marshy meadow, hummock–depression microhabitat, plant properties, soil properties, Yellow River Source Zone

黄河源区丘–洼微生境对高寒沼泽草甸植物群落的影响

摘要：黄河源区高寒沼泽草甸中有许多不均匀的小丘和洼地，形成了独特的微生境，深刻影响着植物特性和土壤养分含量。通过研究高寒湿地冻融丘和洼地空间异质性对植物群落和土壤性质的影响，可以深入了解微地形水文条件对丘–洼微生境空间波动的影响。本研究在黄河源区高寒沼泽湿地的冻融丘(淹水和无淹水)和洼地(蓄水和无蓄水)共设置36个样地(1 m × 1 m)，采集了45个植物样和225个土壤样，

并采用比较法评价高寒沼泽湿地是否存在“肥岛效应”。研究结果显示，冻融丘的存在增加了微生境的空间异质性，促进了藏嵩草群落的物种多样性和土壤肥力。淹水和无淹水的冻融丘生境下的植物高度、盖度、地上生物量、物种丰富度和多样性均显著高于湿地外围的高寒草甸。与高寒草甸相比，高寒沼泽湿地丘-洼复合体为莎草科植物的生长提供了有利的微生境。另外，湿地丘-洼微生境与周围高寒草甸在0–50 cm土层之间的比较表明，土壤有机碳和全氮距离地表越近含量越高。在深层次土壤中，丘洼微生境与高寒草甸土壤养分之间的差距变小。因此，湿地丘-洼微生境形成了一个富饶的“肥沃岛”格局。这些研究结果有助于加深对高寒沼泽草甸生态系统恢复的认识。

关键词：高寒沼泽草甸，丘-洼微生境，植物特性，土壤特性，黄河源区

INTRODUCTION

The Qinghai-Tibet Plateau, in west China, is extensive, with hundreds of thousands of square kilometers of alpine marshy meadows. It has formed through long-term evolution and development under the unique climatic, geographical and geological conditions of the Yellow River Source Zone (YRSZ) (Jin *et al.* 2009; Wei 2019). Alpine marshy meadows are covered with long term or seasonal water and are underlain by permafrost or seasonally frozen soil (Zhang *et al.* 2020). Distributed across the world's highest elevations, they form the largest alpine wetland ecosystem (Gao *et al.* 2013; Li *et al.* 2016) that consists of many hard and dry hummocks rather resistant to low temperatures disturbance than the adjacent alpine meadow (Zhao *et al.* 2020). Hummocks are small dome-shaped (Sharp 1942) cryogenic mounds formed during long-term freeze–thaw cycles, also known as freezing and thawing hummock (Grab 2005; Lin *et al.* 2019; Zhou *et al.* 2019), mainly covered by *Kobresia tibetica*. They are usually closely spaced on flat or gentle slopes (<25°) in wetlands (Grab 2005; Javed *et al.* 2020; Li *et al.* 2017; Zhao *et al.* 2020), and are formed by the joint effects of the frozen soil layer, hydrodynamic forces and growth of plant communities (Grab 2005; Kojima 1994; Li *et al.* 2017; Zhao *et al.* 2020). Hummocks are usually located amid poorly drained depressions. The alternation of hummocks and depressions in close proximity to each other forms a microtopographic feature unique to alpine marshy meadows (Gao *et al.* 2013; Li *et al.* 2016; Lin *et al.* 2019). Especially, hummocks are prominent features of the alpine marshy meadows in the YRSZ. To a large degree, the development of hummocks are closely related to the combined effects of periglacial cryoturbation, hydrodynamics of rivers and lakes in alpine climates and growth of plant communities (Grab 2005; Van Vliet-Lanoë 1991; Zhao 1999). The presence of hummocks in alpine marshy meadows creates spatially heterogeneous heat and moisture conditions (Pintaldi *et al.* 2016; Zhao *et al.* 2020) that in turn, affect the productivity of the alpine meadow vegetation and ecosystems.

Due to the low annual temperature, high elevation, short growing season and slow vegetation growth of the alpine marshy wetland in the YRSZ, it is of great significance to study the influence of the hummock–depression microhabitat on plant biomass and wetland plant communities. Previous studies in alpine marshy meadows have focused on wetland hydrological processes and how they affect the development and evolution of wetlands, maintain and control the function and structure of wetland ecosystems, and change hydrological conditions (Baldwin *et al.* 2001; Javed *et al.* 2020). Research has shown that changes in hydrological conditions (Zhang *et al.* 2020), soil moisture (Scott *et al.* 2008), soil bulk density (Benscoter *et al.* 2005), soil organic matter (Li *et al.* 2017) and soil nitrogen (Biasi *et al.* 2005) have obvious regulatory effects on the structure and characteristics of wetland ecosystems, directly affecting plant growth, competition, species composition and dominance of plant communities (Diamond *et al.* 2019; Whigham and Verhoeven 2009; Yang *et al.* 2014; Yao *et al.* 2014). In comparison, little attention has been paid to the effects of hummock microtopography, even though hummocks significantly influence the spatial distribution of soil nutrients, plant diversity (Dee and Ahn 2012), vegetation dynamics and ecosystem processes (Joseph *et al.* 2014; McGrath *et al.* 2012; Shen *et al.* 2006). The role of hummockUs in alpine marshy meadows is mainly reflected in the improvement of plant community variability and community succession (Zhao *et al.* 2020) via the hummock–depression microhabitat (Ma *et al.* 2020; McGrath *et al.* 2012;

Mu 2019). Differences in hummock–depression microtopography can lead to increase the diversity of plant communities (Pintaldi *et al.* 2016; Zhao *et al.* 2020).

More importantly, the integrated hummock–depression microhabitat of the alpine meadow can have a 'fertile island' effect (Hook *et al.* 1991; Zhao *et al.* 2020). A 'fertile island' refers to a localized concentration of nutrients in the soil at a microscale. In particular, this effect is manifested mainly in the different characteristics between the island's surface soil and the soil adjacent to the island. The difference gradually disappears with soil depth (Hook *et al.* 1991; Kokelj *et al.* 2007; Zhang *et al.* 2011). The differential soil fertility could exert a considerable influence on the alpine meadow vegetation and its ecosystem function, particularly its propensity to degrade. In addition, hummock islands are dry, because they prevent waterlogging, which is also conducive to plant performance and community composition (Biasi *et al.* 2005). Therefore, hummock islands can change plant community structure, species composition and diversity and distribution of soil nutrients, by accelerating the accumulation and circulation of soil nutrients (Diamond *et al.* 2019; Hook *et al.* 1991; Zhao *et al.* 2020).

Due to the hummock–depression complex in alpine marshy meadows is potentially important to the ecosystem function of alpine meadow, the broad aim of this study is to elucidate the variations in vegetation communities and soil properties between freezing and thawing hummocks and depressions in alpine marshy meadows. By examining the changes of vegetation composition and diversity in the hummock–depression microhabitat, we intend to close an existing gap in knowledge and confirm whether the hummock–depression microhabitat can form a 'fertile island' pattern. Moreover, it is necessary to analyze specific locations, especially in alpine wetlands. The specific aims of this work on the hummock–depression microhabitat in the alpine marsh wetland are: (i) to explore the relationship between hummock dimensions (diameter, density and height) and vegetation properties (coverage, height, richness, biomass, diversity and uniformity); (ii) to compare vegetation (importance value [IV], coverage, height and above-ground biomass) and soil properties (temperature, moisture content, organic carbon and total nitrogen [TN]) between hummocks and depressions; (iii) to comparatively assess the relative importance of soil properties and environmental features (e.g. surface water and hummock–depression microtopography) on community composition and (iv) to confirm the existence of soil fertile islands and plant clustering effects in the freezing and thawing hummocks of alpine marshy meadows through field investigations and statistical analyses.

MATERIALS AND METHODS

The study site is located in Maqin County (34°46.1 N, 100°21.4 E, 3680 m a.s.l.), southwestern Qinghai Province in the eastern YRSZ. This area was selected because it contained a widespread representative alpine marshy meadow with numerous hummocks and depressions (Fig. 1). Hummocks form on the surface of the soil, with heights ranging between 5 and 30 cm and maximum diameters between 10 and 96 cm. These alpine hummocks make up approximately 40%–70% of the meadow surface (Gao *et al.* 2020; Zhao *et al.* 2020). The annual temperature averages −2.6 °C, and the average annual precipitation reaches 513 mm, which is mainly concentrated between June and September (Sun *et al.* 2020; Zhao *et al.* 2020). The cold season lasts for 7–8 months each year, during which conditions are windy with heavy snows. Soil starts freezing in middle to late October each year to a depth of 52–220 cm (Sun *et al.* 2020). The frozen layer partially thaws in early and middle May, with the freezing and thawing period lasting up to 180 days each year (Li *et al.* 2013; Sun *et al.* 2020; Wang *et al.* 2015). The rainfall during this period accounts for 92.2% of the annual total. The annual sunshine totals 2576 h (Sun *et al.* 2020). Thus, this area has a cold plateau climate. The hummocks' surface soil (0–10 cm) has a bulk density of 1.07 g/cm^3 with a pH of 6.88. The alpine meadow is dominated by cold-tolerant species such as *K. tibetica*, *Kobresia capillifolia*, *Kobresia humilis* and *Carex scabrirostris* (Sheng *et al.* 2019; Zhao *et al.* 2020).

Measurement of hummock morphometry

To evaluate the hummock–depression microhabitat, three sampling plots of 1 × 10^6 m^2 of typical marshy alpine wetlands with similar geographical conditions were selected, and a similar sampling procedure was carried out in two other marshy alpine wetlands separated by a minimum distance of 5 km. Due to the uniqueness of the hummock morphometry, the traditional plot design would cause large errors (Gurney and Hayward 2015;

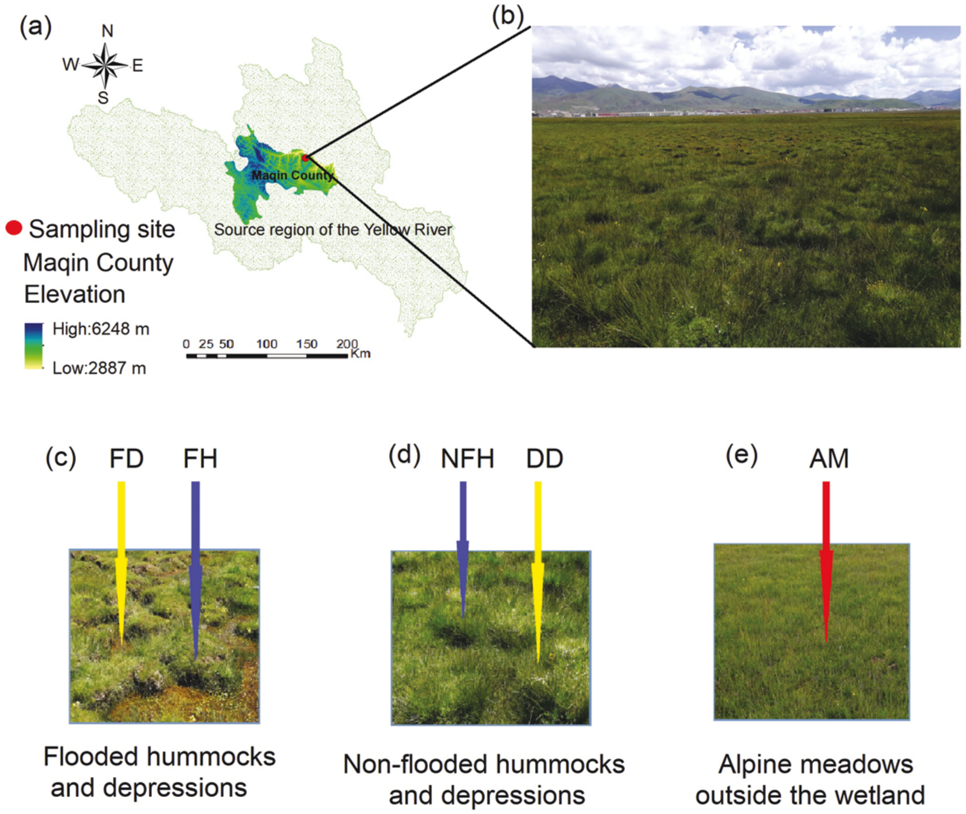


Figure 1: Location of the study site and sites of samples in different parts of the alpine marshy meadow. (**a**) Location of the study site; (**b**) selected area of alpine marshy wetlands; (**c**) FH and depressions; (**d**) NFH and depressions; (**e**) AMs, among them. Among them, FH refer to the depression adjacent to the hummocks that are filled with water throughout the year, and the hummocks are surrounded by water; NFH refer to the depression adjacent to the hummocks that has seasonal water or is in a long-term drought state, and there is no water around the hummocks.

Zhang *et al.* 2018). Therefore, 36 plots with a size of 5 m × 5 m were set up in this study to measure the morphometric characteristics of the hummocks. The distance between each plot was about 35 m. Among them, 18 sites were, respectively, set up flooded (FH) and non-flooded hummocks (NFH) and depressions.

At 18 sites, two smaller sampling areas of 1 m × 1 m in size were randomly selected (one hummock and one depression) for vegetation survey and soil sample collection. Among them, the same area of 20 cm × 20 cm was selected for soil sampling from hummocks top and depressions. In addition, to assess whether the marshy alpine wetland has the 'fertile island' effect, nine additional broad-scale plots (6×10^5 m^2) were set up (e.g. non-wetland alpine meadow or AM). A total of 45 vegetation plots were surveyed, and 225 soil samples were collected in this study.

Fieldwork was conducted in August 2018 and 2019. The morphometric characteristics of hummocks (hummock density, hummock height, hummock diameter, hummock basal area, hummock volume, hummock surface area) were investigated under the optimal conditions for plant growth (Fig. 2). The number of hummocks (N) in a plot was counted, and their basal diameter (BD) and height (H) were measured using a stainless-steel ruler (Fig. 2), from which the height to diameter ratio (HDR), hummock basal area (BA), hummock volume (V) and surface area ratio (SAR) were calculated using the following formulas:

$$\mathrm{HDR} = H/D \tag{1}$$

$$V = \left(\frac{4}{3}\pi H\left(\frac{D}{2}\right)^2\right)/2 \tag{2}$$

$$\mathrm{BA} = V/H \tag{3}$$

$$\mathrm{SAR} = (N \times \mathrm{BA})/25 \tag{4}$$

Hummocks were further separated into perennially flooded (FH) and dry or seasonally flooded (NFH) areas. Similarly, depressions were also grouped into

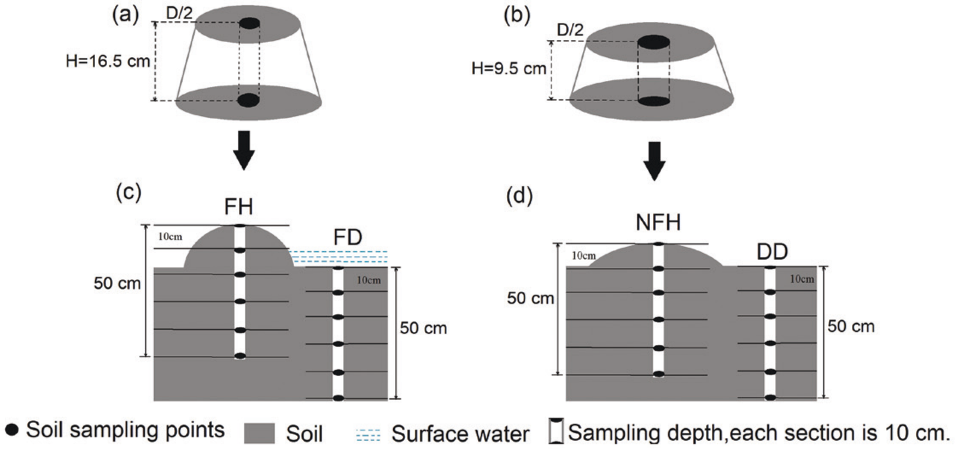


Figure 2: Schematic diagrams illustrating the sampling design for measuring hummock dimensions and collecting soil samples at a sampling point. (**a**) The morphological characteristics of FH; (**b**) the morphological characteristics of NFH; (**c**) a schematic diagram of soil sampling in FH and depressions; (**d**) a schematic diagram of soil sampling in NFH and depressions.

two types, with water (FD) and without (or with seasonal) water (DD), for analyzing community succession and soil fertile islands (Kokelj *et al.* 2007; Zhang *et al.* 2011).

In situ sampling

In each of the 36 plots, temperature and humidity were measured in each of the randomly selected FH and NFH and depressions using a portable three-parameter instrument (FieldScout TDR 350 Soil Moisture Meter with Case, USA) on each layer of the planed surface. The measurement points were set at similar subsampling points (FH and FD, NFH and DD, and AM). In the field, the depth of the surface water in the depressions was measured from the water surface to the ground surface using the polyvinyl chloride (PVC) pipe (2.5 cm inner diameter) method (Wang *et al.* 2016). The pipe, punched with four rows of small, parallel holes (diameter = 5 mm) at an interval of 10 cm, was then inserted vertically into the ground to a depth of 60 cm 1 month in advance. The distance between the water surface in the PVC pipe and the ground surface was measured with a steel ruler. The vertical distance from the PVC pipe end to the depression ground was measured to determine the surface water depth.

In each of the 36 plots, vegetation and soil samples were collected in two subplots with sizes of 1 m × 1 m, one from hummocks and the other from adjacent depressions (Fig. 2). Within each subplot, the main properties of the vegetation community were surveyed, including plant species, grass height, vegetation coverage and above-ground biomass. The last property was sampled by clipping the grass to ground level, separating it by plant species identity and bagging the samples. After heating at 105 °C, the biomass samples were dried at 60 °C to a constant weight (Fang *et al.* 2009). Soil samples were collected using a stainless-steel hand corer with a diameter of 7.5 cm. In total, five soil samples were randomly collected within each of the 36 plots at five depths of 0–10, 10–20, 20–30, 30–40 and 40–50 cm (Fig. 2), together with the temperature and moisture of the surface soil (0–30 cm). After air-drying, the soil samples were ground and sieved through a 200-mesh sieve in the laboratory, from which soil organic carbon (SOC) and TN were analyzed. SOC was analyzed using the dichromate oxidation method (Kalembasa and Jenkinson 1973), and TN was analyzed using the semi-micro Kjeldahl method (Nelson and Sommers 1982).

Data analysis

The field collected plant data were analyzed to derive a number of indicators, ranging from IV to species diversity. IV is an index to reflect the status and function of a species in a plant community, and it shows the dominance and significance of the species (Curtis and McIntosh 1951; Zheng 2009). The IV ranges from 0 to 1. The closer this value is to 1, the higher the dominance and significance of a species in the community; conversely, the closer this value is to 0, the less dominant or insignificant of this species in the community. The IV of an individual plant species was calculated to evaluate the dominance of a species in the community as follows:

$$\mathrm{IV} = (H_\mathrm{r} + D_\mathrm{r} + C_\mathrm{r})/3 \tag{5}$$

where H_r, D_r and C_r refer to the relative height, the relative density and the relative coverage of vegetation, respectively.

Community diversity is a measure of the complexity of community structure and species, and is an important indicator of community stability (Zhang 2015). The level of community diversity mainly depends on the number of species in the community and whether the number of individuals is evenly distributed in each species, i.e. diversity is a function of community richness and uniformity (Zhang 2015; Li 2004). The community diversity was calculated as follows:

$$\text{Shannon–Wiener diversity index } (H') = -\sum_{i=1}^{S} P_i \ln P_i \tag{6}$$

$$\text{Species richness Margalef index } (M_a) = (S-1)/\ln N \tag{7}$$

$$\text{Species uniformity Pielous index } (J) = H'/\ln S \tag{8}$$

where P_i is the proportion of the ith species in the community, S is the number of species in each community and N is the number of species in each sample plot.

Soil properties in the hummocks and depressions were analyzed at five depths. One-way analysis of variance of the difference characteristics of the plant community and soil properties was carried out using a general linear model ($y = \beta_1 x + \beta_0$), followed by a least significant difference *post hoc* test to compare the properties among two pairs of sites with the SPSS 23.0 software (FH and FD, NFH and DD, AM). Linear model redundancy analysis was undertaken to examine the relationships between plant community characteristics and soil properties (Wang *et al.* 2017; Zhao *et al.* 2020) by using the CANOCO software for Windows, version 5.0 (Ter Braak 1998).

RESULTS

Hummock dimensions *vs.* vegetation properties

FH account for 54.02% of all hummocks, and are dominated by *K. tibetica*, with a HDR value of 0.61 (Table 1). NFH account for 14.72% of the total area, and are dominated by *K. humilis*, with a HDR value of 0.27. The base diameter of FH (25.33 cm) is smaller than the average base diameter of all hummocks (30.03 cm) and that of NFH (34.73 cm). The density of FH (64 Pier/25 m^2) is nearly twice that of NFH (32 Pier/25 m^2). As a result, whether depressions are flooded or not directly affect the size of hummocks and their plant species composition.

Furthermore, the plant species richness (n = 18, R^2 = 0.685, P < 0.001, Fig. 3c) and species diversity (n = 18, R^2 = 0.750, P < 0.001) are both positively correlated with hummock diameter (Fig. 3g). Therefore, hummock dimensions play an important role in maintaining the species diversity of the AM. It is worth noting that larger hummocks also result in a lower hummock density (n = 18, R^2 = 0.762, P < 0.001, Fig. 3g) and shorter hummocks (n = 18, R^2 = 0.537, P < 0.001, Fig. 3h). In turn, vegetation height, coverage, biomass and uniformity all decrease significantly with hummock diameter (R^2 > 0.48). Among these plant properties, biomass is the most closely related to hummock diameter due to the larger surface area of the hummock. Therefore, vegetation structure and functional traits related to growth were evaluated by hummock dimension that also affects the performance measures of plants. Hummock dimension is significantly negatively correlated with vegetation height, coverage, aboveground biomass and uniformity, and significantly positively correlated with vegetation diversity and richness (P < 0.05, Fig. 3).

Overall plant community

Vegetation community composition

Hummocks and depressions in the alpine marshy meadow encompass a total of 34 species (seven genera) in the study area (Table 2). The number of species (11) is high in FH, dominated by *K. tibetica* (IV = 0.413), where the main associated species is *K. capillifolia* (IV = 0.189). The number of species increases to 22 in NFH, dominated by *K. humilis* (IV = 0.303)

Table 1: Characteristics of the two classes of flooded and non-flooded alpine hummocks

Types	BD (cm)	Hummock (SAR, %)	Hummock density (Pier/25 m^2)	HDR	Dominant species
FH	25.33 ± 3.97	54.02 ± 0.26	62.00 ± 3.00	0.61	*Kobresia tibetica*
NFH	34.73 ± 5.61	14.72 ± 0.11	32.00 ± 6.00	0.27	*Kobresia tibetica* +*Kobresia humilis*
All	30.03 ± 6.44	24.20 ± 0.19	47.00 ± 16.00	0.42	*Kobresia tibetica*

Mean ± SE; all refers to hummocks.

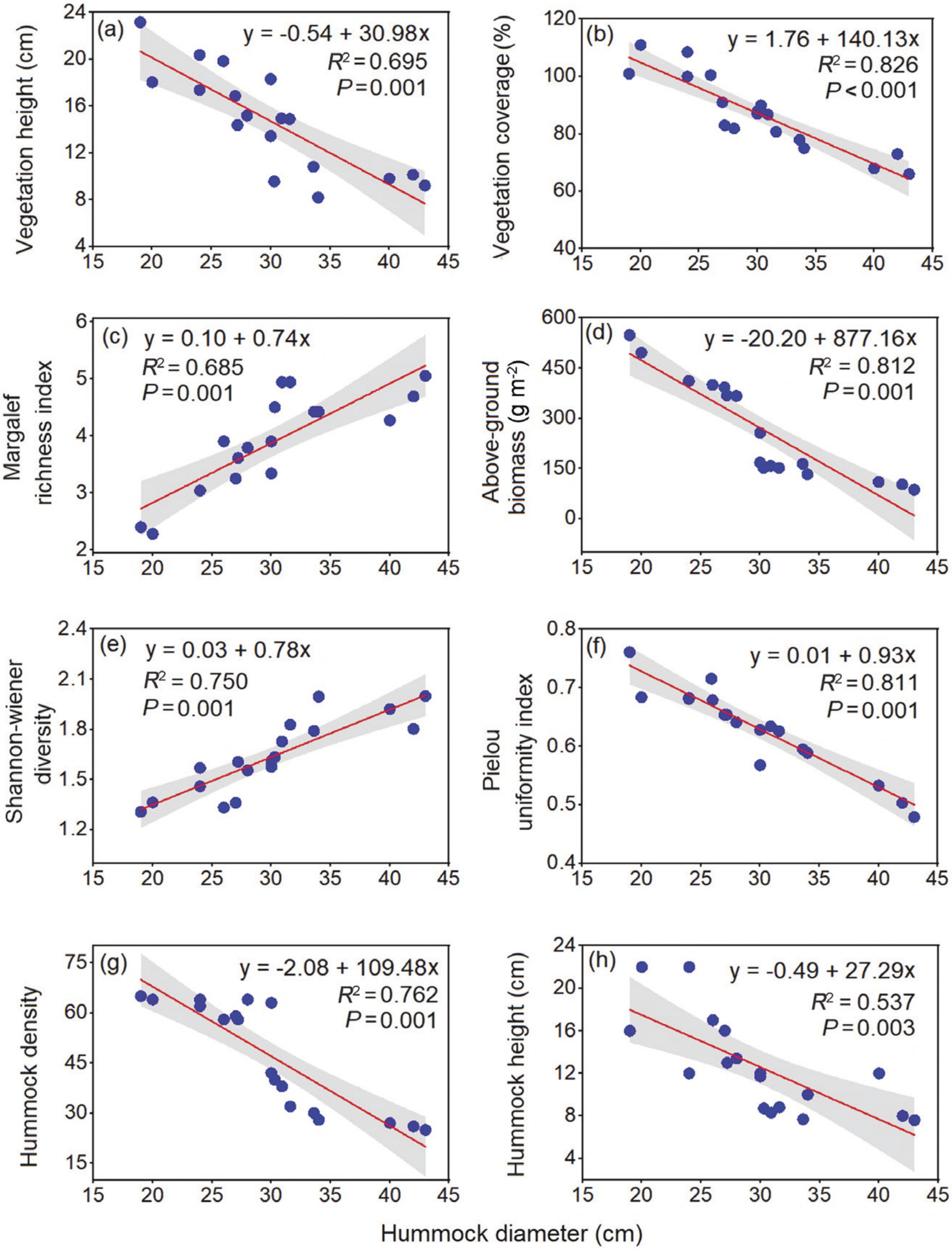


Figure 3: The relationships between hummock diameter and the average (**a**) plant height, (**b**) coverage, (**c**) species richness, (**d**) above-ground biomass, (**e**) species diversity and (**f**) uniformity, and the relationship between hummock diameter and (**g**) density and (**h**) height (gray areas show 95% confidence intervals).

and *K. tibetica* (IV = 0.172), while the main associated species is *Deschampsia cespitosa* (IV = 0.148). However, in the flooded depressions (FD) with accumulated water, the number of species decreases to only 3, dominated by *Carex muliensis* (IV = 0.160). In contrast, there are 11 species in non-flooded depressions (DD) without water accumulation, with the same dominant species *C. muliensis* (IV = 0.134) and the main associated species *C. scabrirostris* (IV = 0.119). However, there are a total of 29 species of plants in the

Table 2: IV of species composition on alpine hummocks

	IV				
Species	**FH**	**FD**	**NFH**	**DD**	**AM**
Kobresia tibetica	0.413		0.172		
Carex scabrirostris		0.095		0.119	0.125
Carex muliensis		0.160		0.134	0.080
Trollius farreri	0.035		0.005		0.039
Caltha palustris	0.055		0.050		0.040
Parnassia trinervis	0.016				0.011
Kobresia capillifolia	0.189				
Polygonum sibiricum	0.033		0.024		0.035
Chamaesium paradoxum	0.044		0.104		0.060
Agrostis hugoniana			0.047		0.047
Deschampsia cespitosa	0.049		0.148		0.057
Kobresia humilis	0.029		0.303		0.096
Halerpestes tricuspis				0.058	0.038
Potentilla anserine			0.025		0.104
Blysmus sinocompressus		0.103		0.083	
Lancea tibetica				0.006	0.008
Cremanthodium discoideum			0.013		0.036
Taraxacum mongolicum				0.007	0.017
Poa pratensis			0.043	0.040	0.068
Stellaria vestita				0.017	0.012
Allium sikkimense	0.032		0.022		0.023
Cremanthodium lineare	0.031		0.023		0.015
Ranunculus japonicas				0.024	
Draba eriopoda			0.026		0.016
Oxytropis ochrocephala				0.012	0.040
Plantago depressa			0.013		0.010
Glaux maritime			0.103		0.047
Gentiana straminea			0.073		0.047
Elymus nutans			0.038		0.107
Koeleria litvinowii			0.044		0.042
Pedicularis rhinanthoides			0.007		0.026
Saussurea stella				0.021	0.017
Potentilla saundersiana			0.004		0.005
Aster asteroids			0.010		

IVs range between 0 and 1. The closer this value is to 1, the higher the dominance and significance of a species in the community; conversely, the closer this value is to 0, the less dominant or insignificant of this species in the community.

alpine meadows outside the wetland (AMs), of which *C. scabrirostris* (IV = 0.125) is the main species, and the main associated species is *Elymus nutans* (IV = 0.107). As surface water disappears from the depressions, the number of species continues to increase. From FH to NFH, the IV of *K. tibetica*, the main species on the hummocks, decreases from 0.413 to 0.172, a decrease of 58.35%, while the IV of *K. humilis* increases from 0.029 to 0.303, an increase of 944.83% (Table 2). From NFH to AM, the IV of *K. humilis* decreases from 0.303 to 0.096, a decrease of 68.32% (Table 2). Finally, this shows that from FH to NFH to AM, with the disappearance of surface water in the depression, the spatial pattern of the community structure has changed, which is caused by the interaction between the two species of Cyperaceae.

Considering all the plants in our entire study area (Fig. 4), six species are from the Cyperaceae family (17.65%); five species are from the Gramineae family (14.71%) and Compositae family (14.71%) each; four species are from the Ranunculaceae family (11.76%); two species are from the Gentianaceae family (5.88%) and Scrophulariaceae family (5.88%) each; one species is from the Fabaceae (2.94%); and there are also nine other families (26.47%). In the FH, Cyperaceae and Gramineae families account for 68.14% and 5.29%, respectively; 36.62% and 24.67% in the NFH; 23.74% and 25.32% in the AMs; and 64.49% and 7.68% in the DD (Fig. 4). In particular, *Carex* spp. plants of Cyperaceae family account for the entire FD. In general, hummocks have more species than depressions. Thus, from the microhabitat of wetland hummocks and depressions to the alpine meadows on the periphery of the wetland, the number of Cyperaceae species gradually decreases, while the number of Gramineae species gradually increases.

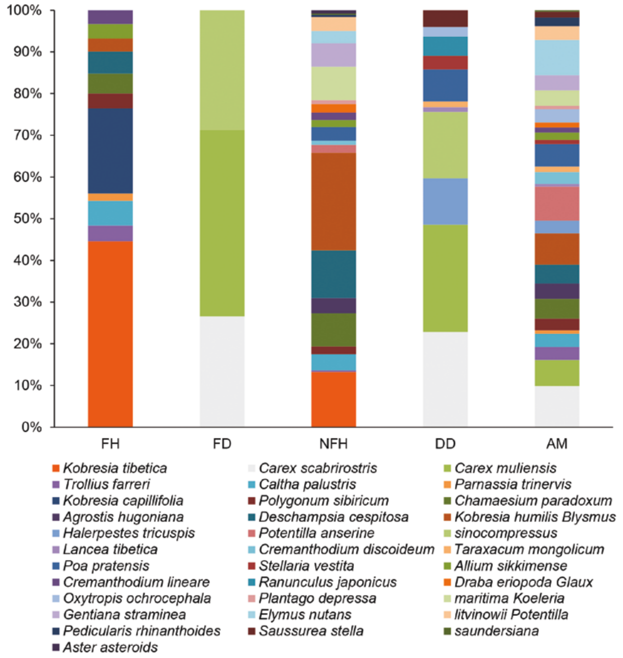


Figure 4: Area percentage stacking histogram of IVs of species composition.

Vegetation properties

Vegetation height and coverage vary with microhabitat, with plants being taller and having greater cover in FH as opposed to NFH ($P < 0.05$, Fig. 5). Vegetation height and coverage in FD are not significantly greater than in FH ($P > 0.05$), but are significantly larger than in NFH, DD and AMs ($P < 0.05$, Fig. 5a and b). Although DD have a higher species richness than FD, the species richness of NFH is higher than that of FH and FD (Fig. 5c), while the species abundance of DD is lower than that in AM. Thus, hummocks are the main contributors to the higher species diversity in seasonal depressions. The average Margalef species richness (M_a) of hummocks at all sampling points is 3.88, which is significantly different from that (1.07) of depressions, while the number of species is 72% higher on hummocks ($P < 0.05$, Fig. 5c). However, AM has the highest species richness and species diversity; both indices are significantly higher than those in NFH, FH and DD ($P < 0.05$, Fig. 5c and d). FH have the highest above-ground biomass, which is significantly higher than that in AM, DD, NFH and FD ($P < 0.05$, Fig. 5e). The plant Pielou uniformity of AM was higher than that in all hummocks and depressions ($P < 0.05$, Fig. 5f).

The influence of microhabitat

Soil properties

The surface soil temperature of NFH and DD is higher than that of FH and FD, and both are higher than that of AMs. But surface soil temperature difference between the wetland and the periphery of the wetland is not significant ($P > 0.05$, Table 3). Therefore, microtopographic hummocks affect the distribution of heat. The surface soil moisture content of depressions is significantly higher than that of hummocks ($P < 0.05$), regardless whether they are flooded or non-flooded. However, the soil moisture content of AM lies between that of NFH and DD, and is significantly different from that of FD ($P < 0.05$). At the same time, SOC of FH and FD is significantly higher than that of NFH and DD ($P < 0.05$), and both

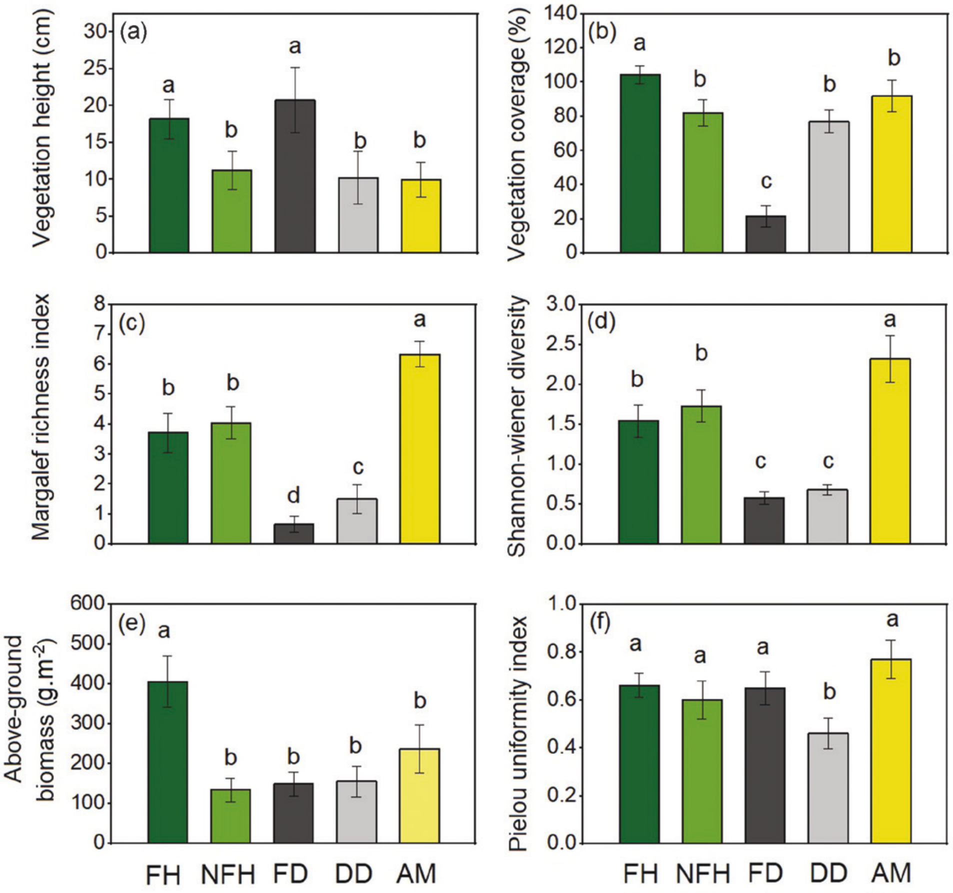


Figure 5: (**a**) Mean vegetation height, (**b**) vegetation coverage, (**c**) species richness, (**d**) species diversity, (**e**) above-ground biomass and (**f**) species uniformity of flooded hummocks (FH), non-flooded hummocks (NFH), depressions between flooded hummocks (FD), depressions between non-flooded hummocks (DD) and alpine meadows (AM) outside the wetland (number of sampling points = 45), among them, the average value refers to mean ± SE.

are significantly higher than that of AM ($P < 0.05$). Thus, surface SOC and TN of alpine wetlands with microtopographic hummocks are significantly higher than those of AMs ($P < 0.05$).

Large differences in SOC exist among the FH and NFH sites (Fig. 6), and the difference in TN is insignificant ($P > 0.05$). But the relative values of SOC and TN remain consistent at all soil depths. Namely, SOC and TN are the highest in the surface layer (0–10 cm) and gradually decrease down from the surface. Both are larger at the FD sites than at the other four sites in every soil layer (Fig. 6a and b). The total concentrations of SOC and TN in the 0–50 cm soil follow the order of FH-FD > NFH-DD > AM (Fig. 6c and d). The presence of water in the depressions is conducive to the accumulation of soil carbon and nitrogen, as are the hummock-triggered fluctuations in surface relief (Biasi *et al.* 2005; Pintaldi *et al.* 2016; Zhao *et al.* 2020). The SOC values in soil layers of 0–10, 10–20, 20–30, 30–40 and 40–50 cm, in FH–depression wetlands are 72.62%, 69.91%, 64.06%, 39.78% and 34.52% higher than those in the AM, respectively, while those values in the NFH–depression wetlands are 66.31%, 61.47%, 55.03%, 24.57% and 18.70% higher than those in AM, respectively. In FH–depression wetlands, TN values are 60.26%, 56.17%, 49.35%, 31.05% and 18.20% higher than those in AM, respectively, while those values in NFH–depression wetlands are 57.37%, 44.29%, 39.83%, 22.96% and 16.24% higher than that in AM, respectively (Fig. 6c and d). The SOC and TN contents of the FH (0–50 cm) are 15.06% and 6.97% higher than those of the NFH, 21.49% and 15.31% higher than those of the DD, but 4.34% and 3.12% lower than those of the FD, and 63.55% and 49.82% higher than those of the AMs on the periphery of the wetland (Fig. 6c and d). The differences in soil nutrients between hummocks and depressions in the same habitat are small (Fig. 6), but these differences are marked between hummocks and depressions in different habitats (Fig. 6; Table 3). The hummock–depression microtopography of the alpine marshy wetland and that of the AMs distant from the wetland are significantly different (Table 3). Especially, in deeper layers, the gap between the soil nutrients in the hummock–depression wetland and the AMs outside the wetland is increasingly bridged.

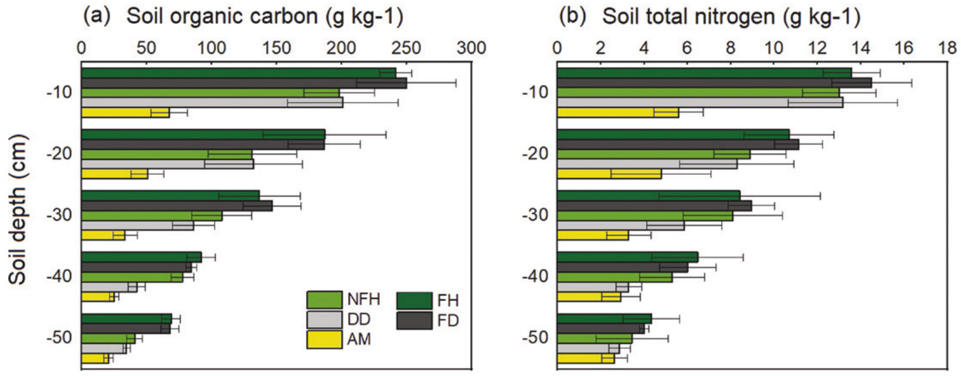
Surface water

The surface water level change of the microhabitat and vegetation characteristics has a good linear relationship. As the surface water level falls, both species richness and diversity increase significantly ($R^2 = 0.62$ and 0.78, $P < 0.01$, Fig. 7a and b). Vegetation coverage, height and above-ground biomass all have significant positive linear correlations with the surface water level ($R^2 \geq 0.71$, $P < 0.01$, Fig. 7c–e), but species uniformity has a weak negative correlation ($R^2 = 0.38$, $P < 0.01$, Fig. 7f). Thus, the deeper the surface water in the alpine marshy wetland, the higher the vegetation coverage, the taller the plants and the greater the above-ground biomass. Conversely, the simpler the community structure, the lower the species richness, uniformity and diversity. Compared with the non-flooded

Table 3: Comparison of soil properties (0–10 cm) between flooded alpine meadow microtopography and dry alpine meadow

	Flooded wetland		Non-flooded wetland		Wetland periphery
	FH	FD	NFH	DD	AM
ST (°C)	16.70 ± 4.76 a	15.97 ± 4.36 a	18.30 ± 4.80 a	18.58 ± 3.83 a	15.39 ± 3.52 a
SMC (%)	55.90 ± 6.02 b	67.86 ± 2.50 a	31.74 ± 8.09 c	54.99 ± 5.71 b	49.97 ± 5.13 b
SOC (g/kg)	241.54 ± 23.18 a	249.98 ± 25.34 a	198.30 ± 25.84 b	201.13 ± 24.74 b	67.29 ± 13.98 c
TN (g/kg)	13.58 ± 1.31 a	14.50 ± 1.85 a	13.01 ± 2.78 a	13.51 ± 2.22 a	5.58 ± 2.13 b

Abbreviations: SMC = soil moisture content, ST = soil temperature. Letters indicate soil temperature, moisture content, organic matter and TN. Different letters indicate significant differences between treatments ($P < 0.05$). Similar letters indicate no significant difference, among which a > b > c.



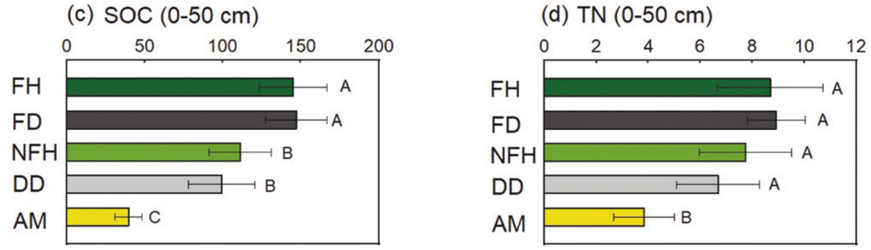


Figure 6: (**a**, **b**) Concentrations of SOC and TN in soil layers (0–10, 10–20, 20–30, 30–40 and 40–50 cm), (**c**, **d**) total concentrations of SOC and TN in the surface soil layer for depths from 0 to 50 cm; number of samples = 225; the units of SOC and TN are g/kg. Capital letters indicate SOC and soil TN. Different letters indicate significant differences between treatments ($P < 0.05$). Similar letters indicate no significant difference, among which A > B > C.

areas, the perennially flooded habitat has a lower plant diversity. As a result, moisture-loving plants are gradually replaced by drought-tolerant plants, causing the richness and species diversity of the plant communities to slowly increase and plant coverage to progressively decrease, with habitat succession.

Surface water is the most important factor in maintaining the health of the alpine marshy wetland and the healthy coexistence of hummocks and depressions (Zhang *et al.* 2020). Fig. 8 shows that SOC and TN of both hummocks and depressions are significantly positively related to surface water level ($R^2 > 0.41$, $P < 0.01$). As the surface water level gradually increases, SOC and TN increase; but SOC and TN decrease. Therefore, SOC and TN in FH and depressions are greater than those in NFH and DD (Fig. 6).

Comparison of two microhabitats

Redundancy ordination analysis reveals the correlations of plant community characteristics with soil properties. In FH, axes 1 and 3 explain 50.37% and 24.34% of the total variation, respectively (Fig. 9). SOC is significantly positively correlated with above-ground biomass ($P = 0.03$) and the sum of the IVs of *K. tibetica* and *K. capillifolia* ($P = 0.04$). In the flooded habitats, the SOC of hummocks is significantly positively correlated with the dominance of *K. tibetica* ($P = 0.02$, Fig. 9a). However, hummock diameter and height (HUH) are insignificantly related to plant community structures (Fig. 9a). In

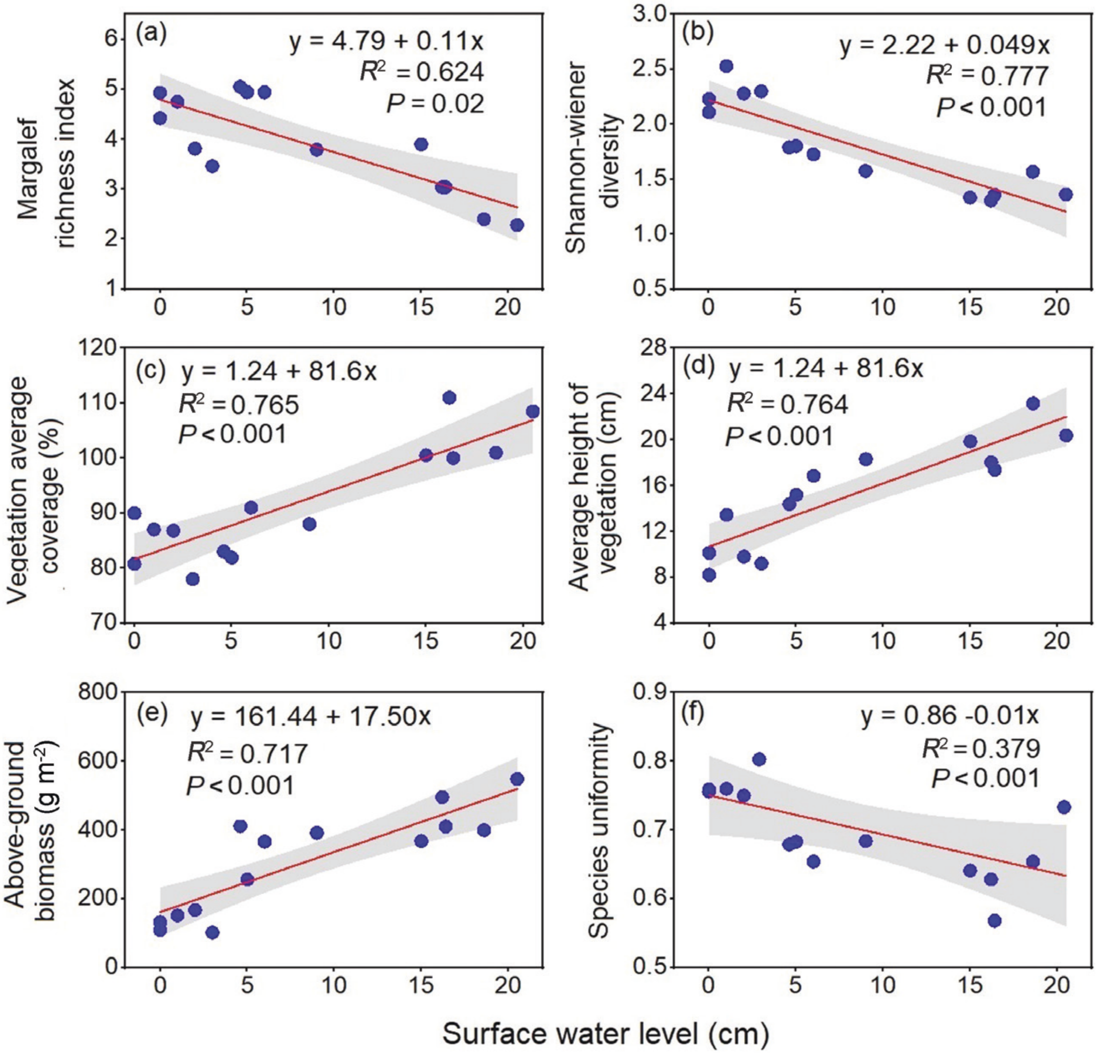


Figure 7: Correlations between the surface water level and (**a**) species richness, (**b**) species diversity, (**c**) mean vegetation coverage, (**d**) mean vegetation height, (**e**) above-ground biomass and (**f**) species uniformity (gray areas are 95% confidence intervals).

non-flooded habitats, the SOC of hummocks related to the Shannon–Wiener diversity ($P = 0.03$), above-ground biomass ($P = 0.02$), Margalef richness (M_a) ($P = 0.04$) of the vegetation and the dominance of *K. tibetica* and *K. humilis* ($P = 0.04$, Fig. 9b); Hummock diameter is significantly positively correlated with the IV of *K. humilis* ($P = 0.01$) and the sum of the IVs of *K. tibetica* and *K. humilis* ($P = 0.04$, Fig. 9b). In these two different habitats, soil moisture is significantly positively correlated with above-ground biomass and the IVs of *K. tibetica*, but the difference in soil temperature ($P = 0.48$, NFH; $P = 0.22$, FH) was insignificant.

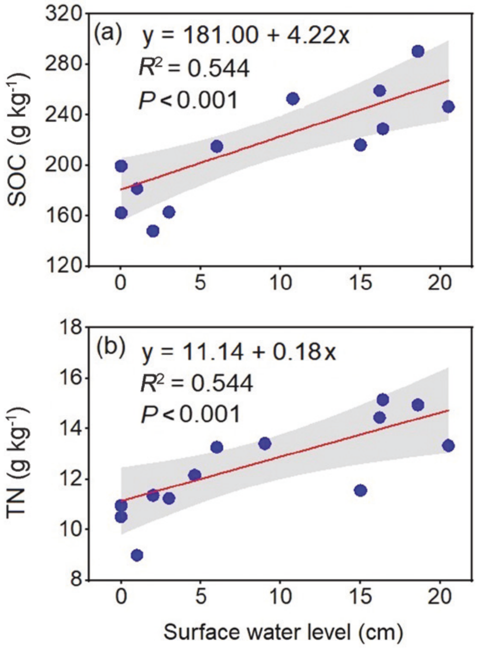


Figure 8: Correlations between the surface water level and the (**a**) SOC and (**b**) TN (gray areas are **95%** confidence intervals).

DISCUSSION

Microscale *vs.* broad-scale plant properties

In this research, the FH and NFH and depressions are considered as hummock–depression microscale features, while the alpine meadows surrounding the wetlands are considered as broad-scale features. The difference between the vegetation community structure observed on the microscale and broad-scale is related to the heterogeneity of the microtopography (Pintaldi *et al.* 2016). In fact, flora surveys show that plant species are selectively distributed in the hummock–depression microtopography of the alpine marshy wetland and the AM (Table 2). On hummocks, *K. tibetica* is dominant; in depressions, *C. muliensis* is dominant; in alpine meadows outside of the wetland, grass is dominant. Namely, the hummock and depression microtopography of the alpine wetland is dominated by species in the Cyperaceae family, while the broad-scale alpine meadows are dominated by species in the Gramineae family, as observed in other areas with similar microtopographic conditions (e.g. Biasi *et al.* 2005; Pintaldi *et al.* 2016). Several plant species create favorable habitats on hummocks due to their heterogeneous microtopography (Pintaldi *et al.* 2016). These microscale spatial patterns of plant distribution can influence the rates of both physical and biogeochemical processes that control habitat ecosystem carbon and nitrogen balance

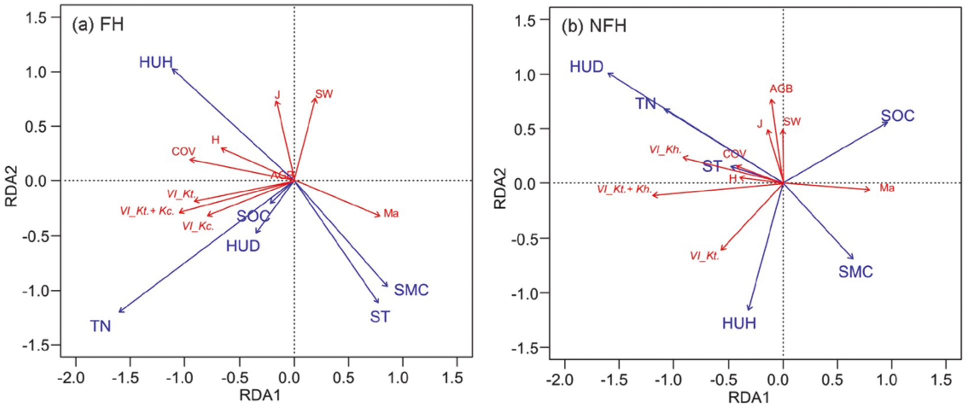


Figure 9: Results of redundancy analysis between FH/NFH and environmental factors. The red lines indicate environmental factors and the blue lines represent vegetation factors. The results of redundancy analysis for soil properties and plant community characteristics in FH (**a**) and NFH (**b**). Abbreviations: AGB = above-ground biomass, HUD = hummock diameter, HUH = hummock height, J = Pielou uniformity index, SMC = soil moisture, ST = soil temperature, SW = Shannon–Wiener diversity, *IV_K.t* = IV of *K. tibetica*, *IV_ K.c* = IV of *K. capillifolia*, *IV_ K.h* = IV of *K. humilis*, *IV_K.t + K.c* = the sum of IVs of *K. tibetica* and *K. capillifolia*, *IV_K.t + K.h* = the sum of IVs of *K. tibetica* and *K. humilis*.

(Oddi *et al.* 2019; Seastedt *et al.* 2001), which in turn affects the growth and survival of plants, and causes different feedbacks between community structure and ecosystem functions (Oddi *et al.* 2019). The leaf traits that Cyperaceae and Gramineae have developed as adaptations for growth and defense in specific environments are strongly linked to litter decomposability (Fabien *et al.* 2007; Saccone *et al.* 2013). Thus, the presence of different dominant species in microscale hummocks and depressions and the broad-scale alpine meadows leads to variability in the plant traits that drive plant decomposition (Oddi *et al.* 2019). Indeed, the functional traits of Cyperaceae and Gramineae are completely different: Cyperaceae plants have the highest water use efficiency, while Gramineae have the highest light use efficiency (Joseph *et al.* 2014; Li *et al.* 2012). In alpine marshy wetland, the hummock–depression microtopography ensures Cyperaceae species can make full use of existing resources to obtain a higher productivity and become the dominant species; and the AMs ensure the availability of existing resources to Gramineae species for them to become the dominant species (Biasi *et al.* 2005; Jackson and Colmer 2005). In other words, the greatest difference between them is the difference in productivity (Jackson and Colmer 2005).

Different flooding conditions in high-elevation areas lead to different habitats and hence different vegetation community structures on hummocks (Pintaldi *et al.* 2016; Zhao *et al.* 2020). Under the same conditions, vegetation species on hummocks and in depressions differ significantly in height, coverage, richness and species diversity (Fig. 3). Therefore, the microhabitat associated with hummocks and depressions may drive plant species composition. Especially, the soil properties and microclimate associated with the microhabitat may also influence plant species composition. Due to the competition between stress-sensitive and stress-tolerant species in non-flooded areas, co-optimal communities are dominant. Heterogeneous microhabitats inevitably lead to changes in soil nutrient content, plant community structure and ecosystem succession (Dwire *et al.* 2004; Enright *et al.* 2005; Gilland and McCarthy 2014). In particular, hummocks generally have a higher productivity and a slower decomposition rate than the adjacent depressions (Pintaldi *et al.* 2016). The decomposition processes bridge the gap between plant community structure and ecosystem functioning by affecting soil properties, which are the main causes of biotic heterogeneity. And soil decomposition plays a crucial role in the aforementioned feedback and, consequently, in vegetation dynamics (Oddi *et al.* 2019). In the same study area, hummock generally have a higher species richness and above-ground biomass, and hence a higher primary productivity than adjacent depressions, as a consequence of high productivity and slow rate of decomposition of *K. tibetica* (Cai *et al.* 2020; Seghieri and Galle 1999) and consequent litter accumulation. Therefore, *K. tibetica* on hummocks also forms extended root systems with comparatively long-lived, slowly decomposing roots (Garner and Steinberger 1989; Zhao *et al.* 2020), which may contribute to the long-term accumulation of SOC in hummock soils. The productivity of wetland vegetation is mainly related to the transport, uptake and reduction of oxygen in soil as affected by soil water content (Grant *et al.* 2012). Depressions have more abundant surface water, which decreases respiration by reducing oxygen uptake used to drive oxidation reduction reactions by soil microbes and roots. Energy yield from oxidation coupled to reduction of oxygen exceeds that from oxidation coupled to reduction of other electron acceptors (Grant *et al.* 2012). Therefore, reduced oxygen uptake slows processes driven by this energy, including microbial and root growth, decomposition and nutrient mineralization, and hence nutrient uptake and plant productivity (Biasi *et al.* 2005; Grant *et al.* 2012; Pintaldi *et al.* 2016). Thus, the greater productivity of hummocks than depressions promotes the flow of water and dissolved nutrients to depressions (Eppinga *et al.* 2009; Pu *et al.* 2020; Wetzel *et al.* 2005). Primary productivity tends to increase with the distance from surface water (Belyea and Clymo 2001). As a result, nutrients are absorbed by vascular plants, which may have a higher plant productivity and litter. Due to the slow decomposition rate of litter, the continuous accumulation of humus enhances the organic carbon content of the hummocky topsoil, resulting in local nutrient concentration effects (Grab 1997; Pintaldi *et al.* 2016). This feedback strengthens the microtopography of the wetland (Grant *et al.* 2012; Pintaldi *et al.* 2016).

To some degree, the differential vegetation community structure between the marshy meadows and AMs is due to the existence of the hummock–depression complex that governs the spatial distribution of water, the most important factor affecting plant characteristics (Peach and Zedler 2006; Vivian-Smith 1997; Wang *et al.* 2016). Water is the most important limiting factor for swamp plants (Wang *et al.* 2016). The perennial presence of water in depressions fosters the development of more fine roots at the bottom of the hummock. Water can recharge nearby hummocks during droughts and create a buffer zone for the plant community (Biasi *et al.* 2005; Pintaldi *et al.* 2016). In contrast, alpine meadows do not have such protection. Therefore, compared with broad-scale AMs, the microhabitat of the hummock–depression complex serves as providers of fertile islands conducive to the growth of Cyperaceae. This microhabitat plays an important role in maintaining the stability of the wetland. Fertile islands beneath *Kobresia* genus are maintained by wind and water erosion processes and complex interactions between plants and the surrounding soil matrix (Cai *et al.* 2020; Garner and Steinberger 1989; Seghieri and Galle 1999; Zhao *et al.* 2020). The fertile island effect may not be a simple result of plant litter and nutrient accumulation (Cai *et al.* 2020; Zhao *et al.* 2020). Rather, the microenvironment is substantially modified as a result of interactions among plant succession (Aguiar and Sala 1999), soil pedogenesis (Pintaldi *et al.* 2016), soil water (Hesp and McLachlan 2000) and freezing–thawing of soil layers (Grab 1994, 2005). In addition, as species diversity rises, the degree of increase in species uniformity is greater than the degree of decrease in interspecies differences, which still leads to an increase in functional diversity (Fig. 5). Species uniformity is the main factor leading to changes in functional diversity. Due to the competitive release effect, the community will gradually replace high-quality Cyperaceae and Gramineae with inferior broad-leaved weeds as a manifestation of degradation. Although the species diversity and functional diversity of AM communities outside the fertile islands also increase, the community structure and the forage value of grasslands have been greatly reduced (Grab 1997; Joseph *et al.* 2014; Mark 1994; Tarnocai and Zoltai 1978). Thus, all these factors help to create and protect the unique vegetation community structure and soil environment of this alpine marshy wetland.

Relative importance of soil and microtopography

The formation of soil heterogeneity in alpine hummocks is initiated by differential frost heave (Grab 2005), rather than erosion and scrub growth in steppe desert ecotones (Luo *et al.* 2016; Zhang *et al.* 2011). In deeper soil layers, the increasingly smaller difference between the wetland hummock–depression microtopography and the soil characteristics of the AM indicate that the wetland hummocks reflect the fertile island effect and that the depressions around the hummocks are the suppliers of water and nutrients for these fertile islands (Fig. 6); thus, hummocks bring organic carbon-rich silt and clay deeper into greater depths under the cryoturbation, which is a necessary condition for the formation and development of hummocks (Grab 2005; Pintaldi *et al.* 2016), which contributes to the long-term accumulation of SOC in the hummocks and is also the reason for the formation of fertile islands. However, due to the influence of climate and human factors, the wetlands are gradually shrinking; the aridification of wetlands has reduced the SOC, TN and soil moisture of the NFH–depression microtopography, compared with flooded areas, and the soil temperature has increased slightly. This change occurs because seasonal accumulations of water or frequent water level fluctuations are more likely to promote the development of the hummock microtopography (Peach and Zedler 2006; van Hulzen *et al.* 2007). Thus, the base diameters of NFH are larger than those of FH (Table 1). A taller hummock enlarges the surface area receiving solar radiation and enables plants to photosynthesize more effectively (Grab 1997; Joseph *et al.* 2014; Wang *et al.* 2016).

Microtopography affects the distribution of soil textures within fertile islands (Grab 1997), which contributes to creating a unique microhabitat to which some plants are better adapted than others and therefore influences the diversity of plant species (Smith *et al.* 2012). Thus, the heterogeneous habitat created by the spatial differentiation of the hummock–depression microtopography has led to a diversified regional species richness and community (Diamond *et al.* 2019). However, the hummock–depression microtopography develops quickly, independent of soil texture, soil moisture and temperature (Biasi *et al.* 2005). Especially, the microtopography exerts an important influence not only on soil physical properties, but also on nutrient and carbon cycling rates, either directly through spatial patterns in climate or indirectly through variations in plant cover, litter quality and quantity (Biasi *et al.* 2005; Fisk *et al.* 2003; Zhao *et al.* 2020). The microtopography retains soil minerals in the slow-moving swamp water and maintains the soil nutrient content (Pintaldi *et al.* 2016). In this study, a larger surface area of a hummock could allow for increases the rate of accumulation and decomposition of organic matter (Belyea and Clymo 2001; Watts *et al.* 2010), creating a fertile island model of soil nutrients. Therefore, the microhabitat created by hummocks plays a primary role in affecting vegetation properties, while soil properties play a secondary role.

CONCLUSIONS

This study shows that as the moisture content of the marshy meadow decreases, the density and HDR of the hummocks gradually decrease, while the coverage, height and above-ground biomass of the vegetation on the hummocks also decrease. In contrast, the abundance and diversity of vegetation gradually increases. The fertile island pattern dominated by *K. tibetica* is gradually succeeded by *K. humilis* and finally by Gramineae. *Kobresia tibetica* is the dominant species in FH, and *K. humilis* is the dominant species in NFH. The increases in species richness and above-ground biomass on hummocks with respect to intervening depressions are attributed to the existence of fertile islands. The microscale hummock–depression complex has higher vegetation coverage, height, above-ground biomass and soil nutrients than the broad-scale meadows because of its richer water content. In areas without stagnant water and with seasonal stagnant water, the community composition is dominated by wet and mesophyte plants; in perennial water areas, aquatic plants are the mainstay. With the increase in surface water, the richness of plant species shows a significant decreasing trend. As the depth of water accumulation decreases, the coverage of hummocks gradually increases, and the species richness also increases.

The microtopography of hummocks and depressions plays an important role in maintaining the species diversity of the marshy meadow. Larger hummocks can host highly diverse plant communities and increase the spatial heterogeneity of the microhabitat, enabling more water-adapted plants to survive. Thus, these research results are helpful for a comprehensive understanding of the maintenance and adjustment process of the microhabitat of the alpine marshy meadow ecosystem in the YRSZ. This understanding serves as valuable evidence for effectively protecting alpine marshy meadows.

Funding

Thank the members of the research team for their kind support in the experiment, and thank the Science and Technology Department of Qinghai Provincial for the funding of the application basic project (2019-ZJ-7035). Discipline Innovation and Introducing Talents Program of Higher Education Institutions (the 111 Project, D18013) and Changjiang Scholars and Innovation Team Development plan (IRT_17R62).

Conflict of interest statement. The authors declare that they have no conflict of interest.

REFERENCES

Aguiar MR, Sala OE (1999) Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends Ecol Evol* **14**:273–277.

Baldwin AH, Egnotovich MS, Clarke E (2001) Hydrologic change and vegetation of tidal freshwater marshes: field, greenhouse, and seed-bank experiments. *Wetlands* **21**:519–531.

Belyea LR, Clymo RS (2001) Feedback control of the rate of peat formation, *Proc R Soc Biol Sci* **268**:1315–1321.

Benscoter BW, Wieder RK, Vitt DH (2005) Linking microtopography with post-fire succession in bogs. *J Veg Sci* **16**:453–460.

Biasi C, Wanek W, Rusalimova O, *et al.* (2005) Microtopography and plant-cover controls on nitrogen dynamics in hummock tundra ecosystems in Siberia. *Arct Alp Res* **37**:435–443.

Cai Y, Yan Y, Xu D, *et al.* (2020) The fertile island effect collapses under extreme overgrazing: evidence from a shrub-encroached grassland. *Plant Soil* **3**:1–12.

Curtis JT, McIntosh RP (1951) An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* **31**:476–496.

Dee SM, Ahn C (2012) Soil properties predict plant community development of mitigation wetlands created in the Virginia Piedmont, USA. *Environ Manage* **49**:1022–1036.

Diamond JS, McLaughlin DL, Slesak RA, *et al.* (2019) Microtopography is a fundamental organizing structure in black ash wetlands. *Biogeosci Discuss* **17**:901–915.

Dwire KA, Kauffman JB, Brookshire EN, *et al.* (2004) Plant biomass and species composition along an environmental gradient in montane riparian meadows. *Oecologia* **139**:309–317.

Enright NJ, Miller BP, Akhter R (2005) Desert vegetation and vegetation-environment relationships in Kirthar National Park, Sindh, Pakistan. *J Arid Environ* **61**:397–418.

Eppinga MB, de Ruiter PC, Wassen MJ, *et al.* (2009) Nutrients and hydrology indicate the driving mechanisms of peatland surface patterning. *Am Nat* **173**:803–818.

Fabien Q, Aurélie T, Lavorel S (2007) Plant traits in a state and transition framework as markers of ecosystem response to land-use change. *Ecol Monogr* **77**:33–52.

Fang JY, Wang XP, Shen ZH, *et al*. (2009) Methods and protocols for plant community inventory. *Biodivers Sci* **17**:533–548.

Fisk MC, Ruether KF, Yavitt JB (2003) Microbial activity and functional composition among northern peatland ecosystems. *Soil Biol Biochem* **35**:591–692.

Gao J, Li XL, Gary B, *et al*. (2013) Geomorphic centered classification of wetlands on the Qinghai-Tibet Plateau, Western China. *J Mt Sci* **10**:632–642.

Gao Z, Hu X, Li XY, *et al*. (2021) Effects of freeze-thaw cycles on soil macropores and its implications on formation of hummocks in alpine meadows in the Qinghai Lake watershed, northeastern Qinghai-Tibet Plateau. *J Soils Sediments* **21**:245–256.

Garner W, Steinberger Y (1989) A proposed mechanism for the formation of fertile islands in the desert ecosystem. *J Arid Environ* **16**:257–262.

Gilland KE, McCarthy BC (2014) Microtopography influences early successional plant communities on experimental coal surface mine land reclamation. *Restor Ecol* **22**:232–239.

Grab SW (1994) Thúfur in the Mohlesi Valley, Lesotho, southern Africa. *Permafr Periglac Process* **5**:111–118.

Grab SW (1997) Thermal regime for a thufa apex and its adjoining depression, Mashai Valley, Lesotho. *Permafr Periglac Process* **8**:437–445.

Grab SW (2005) Earth hummocks (Thúfur): new insights to their thermal characteristics and development in Eastern Lesotho, southern Africa. *Earth Surf Process Landf* **30**:541–555.

Grant RF, Desai A, Sulman BN (2012) Modelling contrasting responses of wetland productivity to changes in water table depth. *Biogeosciences* **9**:4215–4231.

Gurney SD, Hayward S (2015) Earth hummocks in north-east Okstindan, northern Norway: morphology, distribution and environmental constraints. *Nor Geogr Tidsskr* **69**:299–309.

Hesp P, McLachlan A (2000) Morphology, dynamics, ecology and fauna of *Arctotheca populifolia* and *Gazania rigens* nabkha dunes. *J Arid Environ* **44**:155–172.

Hook PB, Burke IC, Lauenroth WK (1991) Heterogeneity of soil and plant N and C associated with individual plants and openings in North American shortgrass steppe. *Plant Soil* **138**:247–256.

Jackson MB, Colmer TD (2005) Response and adaptation by plants to flooding stress. *Ann Bot* **96**:501–505.

Javed Q, Sun J, Azeem A, *et al*. (2020) Competitive ability and plasticity of *Wedelia trilobata* (L.) under wetland hydrological variations. *Sci Rep* **10**:9431.

Jin H, He R, Cheng G, *et al*. (2009) Changes in frozen ground in the Source Area of the Yellow River on the Qinghai–Tibet Plateau, China, and their eco-environmental impacts. *Environ Res Lett* **4**:045206.

Joseph GS, Seymour CL, Cumming GS, *et al*. (2014) Termite mounds increase functional diversity of woody plants in African savannas. *Ecosystems* **17**:808–819.

Kalembasa SJ, Jenkinson DS (1973) A comparative study of titrimetric and gravimetric methods for the determination of organic carbon in soil. *J Sci Food Agric* **24**:1085–1090.

Kojima S (1994) Relationships of vegetation, earth hummocks, and topography in the high arctic environment of Canada. *Polar Biol* **7**:256–269.

Kokelj SV, Burn CR, Tarnocai C (2007) The structure and dynamics of earth hummocks in the subarctic forest near Inuvik, Northwest Territories, Canada. *Arct Antarct Alp Res* **39**:99–109.

Li G, Mu J, Liu Y, *et al*. (2017) Effect of microtopography on soil respiration in an alpine meadow of the Qinghai-Tibetan plateau. *Plant Soil* **421**:147–155.

Li H, Xu D, Du G (2012) The effect of changes in plant community composition on the wetland moisture status on the degradation gradient of alpine marsh wetlands on the Tibetan Plateau. *J Plant Ecol* **36**:403–410.

Li HR (2004) Review on study biodiversity and ecosystem functioning. *Chin J Ecol* **23**:109–114.

Li XL, Xue ZP, Gao J (2016) Dynamic changes of plateau wetlands in Madou County, the Yellow River Source Zone of China: 1990–2013. *Wetland* **36**:299–310.

Li Y, Dong S, Wen L, *et al*. (2013) The effects of fencing on carbon stocks in the degraded alpine grasslands of the Qinghai-Tibetan Plateau. *J Environ Manage* **128**:393–399.

Lin C, Li X, Li H, *et al*. (2019) Distribution characteristics of soil carbon, nitrogen and storage in different degraded alpine marsh wetlands. *Acta Prata Sin* **27**:805–816.

Luo W, Zhao W, Liu B (2016) Growth stages affect species richness and vegetation patterns of nebkhas in the desert steppes of China. *Catena* **137**:126–133.

Ma H, Zhu Q, Zhao X, *et al*. (2020) Assessing ecological conditions of microtopography for vegetation restoration on the Chinese Loess Plateau. *Nat Environ Pollut Technol* **19**:240–249.

Mark AF (1994) Patterned ground activity in a southern New Zealand high-alpine cushion field. *Arct Alp Res* **26**:270–280.

McGrath GS, Paik K, Hinz C (2012) Microtopography alters self-organized vegetation patterns in water-limited ecosystems. *J Geophys Res Biogeosci* **117**:1–19.

Mu X (2019) Differences in the influence of meadow plants on soil properties at the community and population levels in the Qinghai-Tibet Plateau. *Ph.D. Thesis*. Lanzhou University.

Nelson DW, Sommers L (1982) *Total Carbon, Organic Carbon, and Organic Matter. Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties*. Madison, WI: American Society of Agronomy, 539–579.

Oddi L, Celi L, Cremonese E, *et al*. (2019) Decomposition processes interacting with microtopography maintain ecosystem heterogeneity in a subalpine grassland. *Plant Soil* **434**:379–395.

Peach M, Zedler JB (2006) How tussocks structure sedge meadow vegetation. *Wetlands* **26**:322–335.

Pintaldi E, D'Amico ME, Siniscalco C (2016) Hummocks affect soil properties and soil-vegetation relationships in a subalpine grassland (North-Western Italian Alps). *Catena* **145**:214–226.

Pu Y, Ye C, Zhang S, *et al*. (2020) Response of the organic carbon fractions and stability of soil to alpine marsh degradation in Zoige, East Qinghai-Tibet Plateau. *J Soil Sci Plant Nutr* **20**:2145–2155.

Saccone P, Morin S, Baptist F, *et al*. (2013) The effects of snowpack properties and plant strategies on litter decomposition during winter in subalpine meadows. *Plant Soil* **363**:215–229.

Scott MB, Dickinson KJM, Barratt BIP, *et al*. (2008) Temperature and moisture trends in non-sorted earth hummocks and stripes on the old man range, New Zealand: implications for mechanisms of maintenance. *Permafr Periglac Process* **19**:305–314.

Seastedt TR, Walker MD, Bryant DM (2001) Controls on decomposition processes in alpine tundra. In Bowman WD, Seastedt TR (eds). *Structure and Function of an Alpine Ecosystem: Niwot Ridge*. Colorado, NY: Oxford University Press, 222–236.

Seghieri J, Galle S (1999) Run-on contribution to a Sahelian two-phase mosaic system: soil water regime and vegetation life cycles. *Acta Oecol* **20**:209–217.

Sharp RP (1942) Periglacial involutions in northeastern Illinois. *J Geol* **50**:113–133.

Shen H, Tang Y, Washitani I (2006) Morphological plasticity of *Primula nutans* to hummock-and-hollow microsites in an alpine wetland. *J Plant Res* **119**:257–264.

Sheng W, Zhen L, Xiao Y, *et al*. (2019) Ecological and socioeconomic effects of ecological restoration in China's Three Rivers Source Region. *Sci Total Environ* **650**:2307–2313.

Smith ML, Meiman PJ, Brummer JE (2012) Characteristics of hummocked and non-hummocked Colorado riparian areas and wetlands. *Wetl Ecol Manage* **20**:409–418.

Sun JJ, Wang PB, Tong YS, *et al*. (2020) Overload type and optimization of meadow carrying capacity in Maqin County in the Three-River Source Region, China. *J Mt Sci* **17**:112–123.

Tarnocai C, Zoltai SC (1978) Earth hummocks of the Canadian Arctic and subarctic. *Arct Alp Res* **10**:581–594.

Ter Braak CJF (1998) *CANOCO Reference Manual and User's Guide to CANOCO for Windows, Software for Canonical Community Ordination, Version 4.02*. Ithaca, NY: Microcomputer Power.

van Hulzen JB, van Soelen J, Bouma TJ (2007) Morphological variation and habitat modification are strongly correlated for the autogenic ecosystem engineer *Spartina anglica* (common cordgrass). *Estuaries Coasts* **30**:3–11.

Van Vliet-Lanoë B (1991) Differential frost heave, load casting and convection: converging mechanisms; a discussion of the origin of cryoturbations. *Permafr Periglac Process* **2**:123–139.

Vivian-Smith G (1997) Microtopographic heterogeneity and floristic diversity in experimental wetland communities. *J Ecol* **85**:71–82.

Wang CT, Wang GX, Wu PF, *et al*. (2017) Effects of ant mounds on the plant and soil microbial community in an alpine meadow of Qinghai–Tibet plateau. *Land Degrad Dev* **28**:1538–1548.

Wang M, Cao Y, Wang S (2016) Effects of water level and grassland micro-topography on the species diversity of alpine marsh plant communities in Bayinbrook. *Wetl Sci* **14**:635.

Wang X, Dong S, Sherman R, *et al*. (2015) A comparison of biodiversity–ecosystem function relationships in alpine grasslands across a degradation gradient on the Qinghai–Tibetan Plateau. *Rangel J* **37**:45–55.

Watts DL, Cohen MJ, Heffernan JB, *et al*. (2010) Hydrologic modification and the loss of self-organized patterning in the ridge–slough mosaic of the Everglades. *Ecosystems* **13**:813–827.

Wei X (2019) China's Three Rivers Source: green development nourishes the "Chinese Water Tower". *China Rep*:25.

Wetzel PR, van der Valk AG, Newman S, *et al*. (2005) Maintaining tree islands in the Florida Everglades: nutrient redistribution is the key. *Front Ecol Environ* **3**:370–376.

Whigham D, Verhoeven JT (2009) Wetlands of the World: the next installment. *Wetl Ecol Manage* **17**:167.

Yang J, Li E, Cai X, *et al*. (2014) Research progress on wetland plants' response to water level changes. *Wetl Sci* **12**:807–813.

Yao X, Yang G, Wan R, *et al*. (2014) The impact of water level changes on river and lake wetland vegetation. *Lake Sci* **26**:813–821.

Zhang P, Yang J, Zhao L, *et al*. (2011) Effect of *Caragana tibetica* nebkhas on sand entrapment and fertile islands in steppe–desert ecotones on the Inner Mongolia plateau, China. *Plant Soil* **347**:79–90.

Zhang RJ (2015) *Fundamentals of Ecology*. Beijing, China: Science Press, pp.93–139.

Zhang S, Zhang F, Shi Z, *et al*. (2020) Sources of seasonal wetland methane emissions in permafrost regions of the Qinghai-Tibet Plateau. *Sci Rep* **10**:7520.

Zhang Y, Ma X, Liu X, *et al*. (2018) Preliminary study on morphology, development process and peat accumulation rate of palsas during the Holocene in the Altai Mountains, northern Xinjiang Autonomous Region, Northwest China. *Quat Sci* **38**:1221–1232.

Zhang Y, Wang H, Zhang D (2020) Analysis of the differences in soil physical and chemical properties between two habitats of alpine meadows in the western Sichuan Plateau. *Grassl Sci J* **28**:207–212.

Zhao H, Wei D, Yan Y, *et al*. (2020) Alpine hummocks drive plant diversity and soil fertile islands on the Tibetan Plateau. *Wetlands*:1–11.

Zhao KY (1999) *Mires in China*. Science Press, Beijing.

Zheng FY, Wang YS, Shangguan TL (2009) The Problems of Importance Value Calculation and Their Solutions in Quantitative Vegetation Ecology. In: *International Institute of Applied Statistics Studies, Qingdao, China*, p.530–534.

Zhou B, Li S, Li F, *et al*. (2019) Plant functional groups asynchrony keep the community biomass stability along with the climate change—a 20-year experimental observation of alpine meadow in eastern Qinghai-Tibet Plateau. *Agric Ecosyst Environ* **282**:49–57.