

Synergies between mini-patches of plant communities and steady-stage alpine meadows on the Qinghai-Tibet Plateau

li lin¹, Xingliang Xu², guangmin cao¹, Fawei Zhang¹, Yikang Li¹, and Junjie Huang³

¹Northwest Institute of Plateau Biology Chinese Academy of Sciences

²Institute of Geographic Sciences and Natural Resources Research Chinese Academy of Sciences

³School of Mechanical and Power Engineering Henan Polytechnic University Jiaozuo China 454000

September 12, 2022

Abstract

Mini-patches are considered indicators of an ecosystem's response to interference, particularly those in alpine meadow ecosystems. Thus, monitoring the characteristics of mini-patches can elucidate the organization of an ecosystem's components, the strategies it employs to survive interference, and the mechanisms whereby it maintains stability. In this research, we used multivariate statistical analysis methods to investigate the characteristics of the plant community and the micro-topography of mini-patches in alpine meadows on the Qinghai-Tibet Plateau from August 2012 to August 2013. Our findings show that (1) mini-patches were distributed in alpine meadows with different levels of degradation and the effects of meteorological characteristics (accumulated temperature above 0°C and accumulation of precipitation) and geographical characteristics (altitude, longitude, and latitude) contributed less than 20% to their distribution and characteristics; (2) alpine meadows maintained aboveground biomass within a certain range under a relative larger range of grazing intensity, illustrating their ability to regulate community structure and components under various intensities of disturbance and showing that alpine degradation could itself counteract grazing disturbance; and (3) overgrazing is the main driver of multi-steady stage coexistence in alpine meadows, as the mini-patches that remain involved in plant community succession function, and as a source of germplasm in the plant community regime shift under different grazing intensities damaged alpine meadows.

Synergies between mini-patches of plant communities and steady-stage alpine meadows on the Qinghai-Tibet Plateau

Li Lin 1, 2, Xingliang Xu 3*, Guangmin Cao 1, Fawei Zhang 1, Yikang Li 1, Junjie Huang 4

1 Northwest Institute of Plateau Biology and Chinese Academy of Sciences, Xining, China, 810008

2 University of Chinese Academy of Sciences, Beijing, China, 100049.

3 Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China, 100101

4 School of Mechanical and Power Engineering, Henan Polytechnic University, Jiaozuo, China, 454000

* Correspondence: xuxl@igsnrr.ac.cn.

Founder: Natural Science Foundation of Qinghai (2020-ZJ-720)

Abstract:

Mini-patches are considered indicators of an ecosystem's response to interference, particularly those in alpine meadow ecosystems. Thus, monitoring the characteristics of mini-patches can elucidate the organization of an ecosystem's components, the strategies it employs to survive interference, and the mechanisms whereby it maintains stability. In this research, we used multivariate statistical analysis methods to investigate the characteristics of the plant community and the micro-topography of mini-patches in alpine meadows on the Qinghai-Tibet Plateau from August 2012 to August 2013. Our findings show that (1) mini-patches were distributed in alpine meadows with different levels of degradation and the effects of meteorological characteristics (accumulated temperature above 0°C and accumulation of precipitation) and geographical characteristics (altitude, longitude, and latitude) contributed less than 20% to their distribution and characteristics; (2) alpine meadows maintained aboveground biomass within a certain range under a relative larger range of grazing intensity, illustrating their ability to regulate community structure and components under various intensities of disturbance and showing that alpine degradation could itself counteract grazing disturbance; and (3) overgrazing is the main driver of multi-steady stage coexistence in alpine meadows, as the mini-patches that remain involved in plant community succession function, and as a source of germplasm in the plant community regime shift under different grazing intensities damaged alpine meadows.

Keywords:

Mini-patch, alpine meadow degradation, succession process, overgrazing, multi-steady stage

Introduction

The alpine meadows that occupy more than 35% of the total area of the Qinghai-Tibet Plateau are the main location of alpine livestock husbandry in the area, particularly because of their use as winter and spring pastures (Zhang et al., 2003). The health of such alpine meadows must be measured to enable estimation of the capacity of ecosystem services, such as water and soil conservation and carbon sequestration (Yang, 2002). In recent years, these alpine meadows have undergone succession into multi-steady stages due to disturbances arising from climate change and excessive human activity (Meng et al., 2014). Given the unique household contract system implemented on family ranches on the Qinghai-Tibet Plateau, the landscape has fragmented into multiple succession stages or steady states, resulting in multi-steady stage coexistence within each topographical and climate area (Cao et al., 2007).

Ecosystem succession processes always proceed sequentially, such that the corresponding plant communities organize into a series of hierarchical structures or discrete levels (Jørgensen et al., 2016; Wellemeyer et al., 2019). Livestock grazing is the primary form of disturbance that affects plant community structure, physical and chemical soil properties, and the ability of alpine meadows to maintain ecological and productive stability (Proulx et al., 1998; Yang et al., 2001). In addition, the effects of livestock grazing on plant-soil system organization are complex (Nicola et al., 2010). For example, long-term and high-intensity grazing can affect plant community structure and composition and even trigger the plant community to regime shift (Lin et al., 2022). Such grazing can also alter the accumulation and transformation of nutrients above and below the ground and influence the micro-climate and micro-geomorphology of mini-patches (Gonzalez et al., 2010). Most prior studies have observed that the intensity of livestock grazing and the reaction of a plant community to grazing are coupled to various conditions (Wedin & Tilman, 1996; Klinerová & Dostal, 2020; Lauren, 2018), which means that the examination of mini-patches can be used to evaluate plant communities and predict the trends of plant community succession (Wu et al., 2012).

Compared with other parts of ecosystems, mini-patches are more sensitive and exhibit greater variations in response to disturbance and can thus be considered as indicators of how ecosystems respond to disturbance. Monitoring the characteristics of mini-patches can thus reveal the organizational components of an ecosystem, the survival strategies used by an ecosystem's plant community to cope with disturbance, and the mechanisms whereby an ecosystem maintains its stability. Mini-patches in alpine meadows can therefore be considered as the basic units of the plant-soil system at fine spatial scales, with their features isolated in function but correlated in space. Consequently, the study of mini-patches in alpine meadows can provide answers to many key questions. For example, are the same types of mini-patches distributed across alpine meadow area of

different grazing intensities or only in areas of certain grazing intensities? What factors mainly influence mini-patch distribution and determine the direction of plant community succession in alpine meadows?

In this research, we aimed to improve understanding on the stabilization mechanisms of alpine meadow ecosystems and strengthen theories on restoration management in multi-steady-state coexistence conditions. Therefore, we explored and examined the factors affecting alpine meadow ecosystems under various grazing regimes by studying the characteristics of plant functional groups and topography in mini-patches and grazing intensity in typical alpine meadows on the Qinghai-Tibet Plateau.

1 Materials and methods

1.1 Study area and sampling method

We chose 109 sampling sites located in the autonomous prefectures of Haibei, Yushu, Guoluo, Haixi, and Hainan in China (Table 1). The meteorological characteristics of accumulated temperature above 0°C and accumulated precipitation over the growing season (mainly in May to September) were respectively 659.1 to 1228.4°C and 257.5 to 693.7 mm in all of the sampling sites. The vegetation type was classified as cold, wet-rainy tundra and alpine meadow according to the Comprehensive and Sequential Classification System of Grassland, and as alpine meadow according to the passive-active degradation process hypothesis (Cao et al., 2007). However, the sampled alpine meadows were in different steady stages (Cao et al., 2007), so we classified the corresponding sample sites according to the characteristics of their plant community, mattic epipedon, and topography into seven steady-stage types of meadow: Gramineae-*Kobresia* meadow, Gramineae-*K. humilis* to *K. pygmaea* transitional meadow, healthy mattic epipedon in *K. pygmaea* meadow, thickening mattic epipedon in *K. pygmaea* meadow, cracking mattic epipedon in *K. pygmaea* meadow, eroded mattic epipedon in *K. pygmaea* meadow, and black-soil beach meadow (Table 1). In view of the fact that the quantitative characteristics of plant communities are prone to reciprocating changes under different grazing intensity, so we divided the meadows into five categories, namely Gramineae-*Kobresia* meadow and Gramineae-*K. humilis* to *K. pygmaea* transitional meadow as “A”, healthy mattic epipedon in *K. pygmaea* meadow and thickening mattic epipedon in *K. pygmaea* meadow as “B”, cracking mattic epipedon in *K. pygmaea* meadow as “C”, eroded mattic epipedon in *K. pygmaea* meadow as “D”, and black-soil beach meadow as “E”.

Table 1. Latitude, longitude, and altitude of sampling sites and their stability stages

Code	Longitude	Latitude	Altitude (m)	Steady stage
1	101°44'56"	34°39'52"	3596	Gramineae- <i>Kobresia</i> meadow
2	100°51'57"	34°58'19"	3802	Gramineae- <i>Kobresia</i> meadow
3	100°29'32"	34°21'29"	3948	Gramineae- <i>Kobresia</i> meadow
4	99°54'47"	33°34'28"	4067	Gramineae- <i>Kobresia</i> meadow
5	95°29'24"	34°5'24"	4306	Gramineae- <i>Kobresia</i> meadow
6	94°33'0"	34°30'0"	4316	Gramineae- <i>Kobresia</i> meadow
7	99°32'14.34"	37°4'2.58"	3233	Gramineae- <i>Kobresia</i> meadow
8	101°18'57"	37°36'47"	3200	Gramineae- <i>Kobresia</i> meadow
9	101°17'52.02"	37°37'13.26"	3204	Gramineae- <i>Kobresia</i> meadow
10	96°55'40.56"	32°51'59.4"	3982	Gramineae- <i>Kobresia</i> meadow
11	100°12'47.22"	34°27'47.1"	3740	Gramineae- <i>Kobresia</i> meadow
12	101°2'31.14"	37°35'24.48"	3171	Gramineae- <i>Kobresia</i> meadow
13	101°27'09"	35°4'56"	3725	Cracking mattic epipedon in <i>K. pygmaea</i> meadow
14	100°51'53"	34°58'13"	3786	Thickening mattic epipedon in <i>K. pygmaea</i> meadow
15	100°34'19"	34°20'23"	4081	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
16	100°29'33"	34°21'57"	3955	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
17	100°16'51"	34°25'16"	3768	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
18	100°24'21"	34°28'42"	4328	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
19	100°16'22"	34°23'37"	3820	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow

Code	Longitude	Latitude	Altitude (m)	Steady stage
20	100°36'34"	34°19'47"	4151	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
21	100°5'6"	34°4'6"	4292	Thickening mattic epipedon <i>in K. pygmaea</i> meadow
22	100°5'28"	34°1'15"	4252	Thickening mattic epipedon <i>in K. pygmaea</i> meadow
23	99°42'16"	33°48'26"	3974	Thickening mattic epipedon <i>in K. pygmaea</i> meadow
24	100°55'9"	35°42'50"	3370	Cracking mattic epipedon <i>in K. pygmaea</i> meadow
25	99°25'8"	33°45'6"	4012	Thickening mattic epipedon <i>in K. pygmaea</i> meadow
26	100°33'53"	32°46'36"	4207	Thickening mattic epipedon <i>in K. pygmaea</i> meadow
27	100°51'7"	30°17'28"	4401	Thickening mattic epipedon <i>in K. pygmaea</i> meadow
28	100°3'42.00"	33°25'51"	4235	Thickening mattic epipedon <i>in K. pygmaea</i> meadow
29	100°23'9"	33°16'5"	4111	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
30	98°7'21"	34°46'6"	4328	Thickening mattic epipedon <i>in K. pygmaea</i> meadow
31	98°41'41"	37°31'53"	3642	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
32	97°10'06.42"	33°50'12.3"	4425	Thickening mattic epipedon <i>in K. pygmaea</i> meadow
33	96°10'48"	33°10'48"	4417	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
34	96°1'12"	33°20'24"	4303	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
35	95°25'12"	33°29'24"	4232	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
36	95°28'48"	34°3'36"	4219	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
37	95°30'36"	34°4'12"	4219	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
38	95°30'36"	34°4'48"	4432	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
39	100°45'9.72"	37°1'19.2"	3350	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
40	100°45'10.32"	37°1'21.96"	3336	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
41	100°22'42.9"	37°54'18.66"	3686	Thickening mattic epipedon <i>in K. pygmaea</i> meadow
42	100°22'32.04"	37°54'27.84"	3691	Thickening mattic epipedon <i>in K. pygmaea</i> meadow
43	100°15'26.76"	38°0'21.06"	3985	Thickening mattic epipedon <i>in K. pygmaea</i> meadow
44	99°23'04.74"	38°35'43.38"	3436	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
45	99°23'02.7"	38°35'39.96"	3428	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
46	100°53'54"	37°57'55"	3335	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
47	101°2'56"	37°52'18"	3527	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
48	101°15'28"	37°42'08"	3278	Cracking mattic epipedon <i>in K. pygmaea</i> meadow
49	101°10'56"	37°40'54"	3239	Thickening mattic epipedon <i>in K. pygmaea</i> meadow
50	101°10'38.28"	37°40'9.3"	3241	Thickening mattic epipedon <i>in K. pygmaea</i> meadow
51	95°59'45.06"	34°36'20.58"	4250	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
52	97°19'38.34"	33°22'31.56"	4255	Cracking mattic epipedon <i>in K. pygmaea</i> meadow
53	97°19'47.7"	33°22'33.9"	4247	Cracking mattic epipedon <i>in K. pygmaea</i> meadow
54	96°55'39.12"	32°51'56.04"	3988	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
55	96°41'41.52"	33°7'41.82"	4370	Thickening mattic epipedon <i>in K. pygmaea</i> meadow
56	96°10'10.38"	33°24'34.68"	4504	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
57	95°8'13.32"	34°43'12.36"	4507	Cracking mattic epipedon <i>in K. pygmaea</i> meadow
58	95°20'51.18"	34°33'41.16"	4234	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
59	95°20'51.36"	34°33'10.32"	4229	Thickening mattic epipedon <i>in K. pygmaea</i> meadow
60	94°49'48.42"	34°53'21.06"	4531	Cracking mattic epipedon <i>in K. pygmaea</i> meadow
61	100°8'11.1"	34°22'32.94"	3934	Gramineae- <i>K. humilis</i> to <i>K. pygmaea</i> transitional meadow
62	99°48'11.82"	33°55'11.58"	4185	Cracking mattic epipedon <i>in K. pygmaea</i> meadow
63	99°14'59.94"	33°22'22.5"	4320	Cracking mattic epipedon <i>in K. pygmaea</i> meadow
64	99°54'16.2"	33°34'16.44"	4082	Thickening mattic epipedon <i>in K. pygmaea</i> meadow
65	101°16'32"	35°17'52"	3580	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
66	101°16'17"	35°17'32"	3580	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
67	101°19'31"	35°16'59"	3635	Black-soil beach meadow
68	101°44'08"	34°39'06"	3593	Black-soil beach meadow
69	100°52'02"	34°58'27"	3800	Eroded mattic epipedon <i>in K. pygmaea</i> meadow

Code	Longitude	Latitude	Altitude (m)	Steady stage
70	100°34'19"	34°20'24"	4084	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
71	100°29'47"	34°21'9"	3957	Black-soil beach meadow
72	100°16'8"	34°25'57"	3772	Black-soil beach meadow
73	100°8'9"	34°9'2"	4089	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
74	100°8'9"	34°9'19"	4091	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
75	100°36'27"	34°19'42"	4145	Black-soil beach meadow
76	100°5'07"	34°4'55"	4212	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
77	99°48'35"	33°55'20"	4189	Black-soil beach meadow
78	99°48'38"	33°55'26"	4203	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
79	99°42'10"	33°48'06"	3956	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
80	100°13'07"	33°28'23"	4299	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
81	100°12'59"	33°23'28"	4288	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
82	99°23'23"	33°34'23"	4077	Black-soil beach meadow
83	99°54'31"	33°34'6"	4078	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
84	99°25'34"	33°45'21"	4009	Black-soil beach meadow
85	99°10'5"	34°18'16"	4219	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
86	100°33'50"	32°46'35"	4232	Black-soil beach meadow
87	100°33'42"	32°46'32"	4257	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
88	100°29'51"	33°23'25"	3912	Black-soil beach meadow
89	100°29'36.6"	33°23'10"	3900	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
90	100°51'07"	33°17'28"	4401	Black-soil beach meadow
91	100°51'7"	33°17'31"	4420	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
92	98°55'57"	34°56'29"	4435	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
93	98°0'40"	34°37'18"	4239	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
94	98°0'56"	34°37'26"	4131	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
95	98°4'20"	35°0'48"	4237	Black-soil beach meadow
96	97°59'6"	34°31'35.4"	4330	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
97	97°48'46.02"	34°13'42.6"	4674	Black-soil beach meadow
98	95°30'36"	34°4'48"	4428	Black-soil beach meadow
99	97°59'48.12"	34°36'20.16"	4255	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
100	96°41'42.78"	33°7'41.28"	4373	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
101	96°10'10.68"	33°24'35.04"	4503	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
102	95°8'13.32"	34°43'12.36"	4507	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
103	94°49'47.76"	34°51'18.6"	4518	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
104	100°29'34.02"	34°21'58.44"	3968	Black-soil beach meadow
105	99°14'8.64"	33°22'20.28"	4077	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
106	99°54'15.6"	33°34'18"	4082	Black-soil beach meadow
107	99°12'9.84"	33°26'8.7"	4321	Eroded mattic epipedon <i>in K. pygmaea</i> meadow
108	99°12'7.44"	33°26'7.98"	4318	Black-soil beach meadow
109	101°1'11.22"	37°37'6.36"	3142	Black-soil beach meadow

Sampling was performed in August in 2012-2013 along 100-m transects within every sampling site that each contained eight evenly distributed 50 cm × 50 cm quadrats. The plant community was divided into five functional groups: Gramineae, Cyperaceae, forbs, Leguminosae, and shrubs. In each quadrat, we recorded the coverage and dry aboveground biomass of plant functional groups, the thickness of the mattic epipedon, and the slope aspect, position, and angle. We also noted the number of livestock grazing at each sampling site (Lin, 2017).

1.2 Sample collection and preparation

The plant samples were placed in an envelope after collection and subsequently baked at 60–80°C for 48 to 72 h to a constant weight, which was then recorded.

An unstructured questionnaire was used to determine the area of the pasture, the type and quantity of grazing livestock, and the grazing time. According to the conversion ratio of 4 sheep equal to 1 yak, the stocking capacity of the pasture was calculated (Xu, 1994), and the stocking capacity was divided into 5 grades. The average grazing intensities per grazing season were 0.00 sheep/ha for more than 1 year, less than 3.65 sheep/ha, 3.65 to 7.50 sheep/ha, 8.25 to 13.00 sheep/ha, and more than 13.00 sheep/ha. In most of the time when the alpine meadow degradation into Black-soil beach meadow would become to no grazing in the pasture, so we investigated the possible grazing intensity used in the past as the average grazing intensity of the pasture.

1.3 Data analysis

The plant functional group characteristics of mini-patches were determined by calculating the average coverage, dry aboveground biomass, and importance value of each plant functional group in each mini-patch (Lin, 2017). The data collected from every mini-patch were also used to calculate the niche breadths of plant functional groups based on the Levins index (Lin, 2017), and mean and standard error on the biomass aboveground, the importance and the niche breadth were calculated by performing a one-way analysis of variance in SPSS Statistics Software (19.0). The probability of each mini-patch reaching a certain multi-steady stage was calculated as the ratio of the environmental characteristics in a single quadrat to the total in all quadrats. The coupling between the plant functional groups of all mini-patch and each environmental factor was calculated via a redundancy analysis (RDA) in R3.6.1 software.

2 Results

2.1 Characteristics of plant functional groups in mini-patches

The aboveground primary production of alpine meadows depended more on their steady stage than on their geographical location or on climate factors. The aboveground primary production was significantly higher under zero grazing and light grazing intensity than under a heavy grazing intensity. The aboveground biomass also differed by grazing intensity. The aboveground biomass of Gramineae, Cyperaceae, and Leguminosae functional groups significantly decreased as grazing intensity increased, while the aboveground biomass of forbs, which were dominant or subdominant in most steady stages, remained relatively stable across grazing intensities. Nonetheless, the total productivity of alpine meadows remained stable across a large range of grazing intensities and a large spatial scale (Fig. 1).

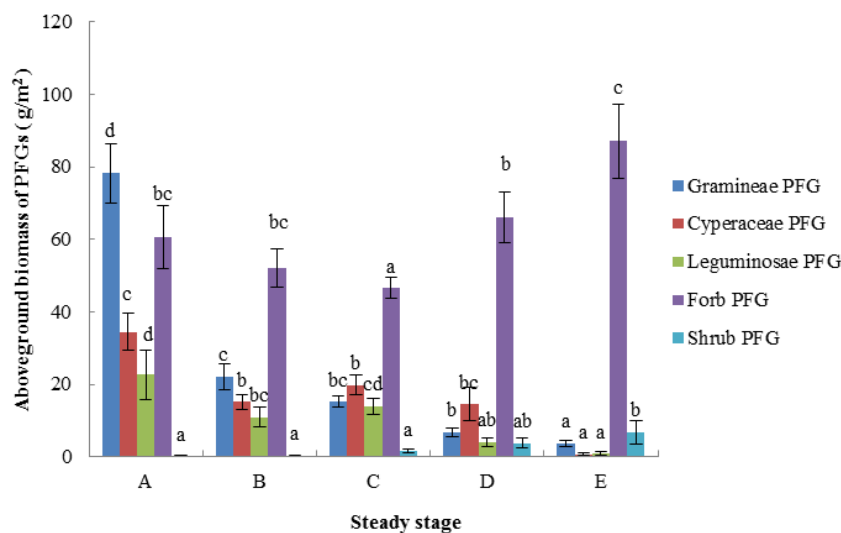


Fig. 1. Aboveground biomass of plant functional groups (PFGs) in mini-patches at various steady stages

Note: A, B, C, D, and E represent Gramineae–*Kobresia* meadow and Gramineae–*K. humilis* to *K. pygmaea* transitional meadow; healthy and thickening mattic epipedon in *K. pygmaea* meadow; cracking mattic epipedon in *K. pygmaea* meadow; eroded mattic epipedon in *K. pygmaea* meadow and black-soil beach meadow, respectively; a, b, c, d represent significance of each biomass of PFG among different steady stages.

The importance of plant functional groups in mini-patches could reflect their ability of resource obtaining positions in the plant community. The importance of Gramineae, Cyperaceae and Leguminosae gradually decreased, that of forbs gradually increased, and shrub kept in a relative stabilization under increasing grazing intensity. The trends in plant functional groups differed and could be divided into three successional periods by estimating the importance in each mini-patch. In the first period, which was under zero or light grazing intensity, Gramineae dominated and the structure of the alpine meadows was that of a grazing climax community. The second period was a transition period in which Cyperaceae was dominance. The third stage was the black-soil beach stage in which Gramineae and Cyperaceae were minor groups and forbs became the dominant group in the plant community, and during this process the Leguminosae had the analogous reaction to Gramineae (Fig. 2).

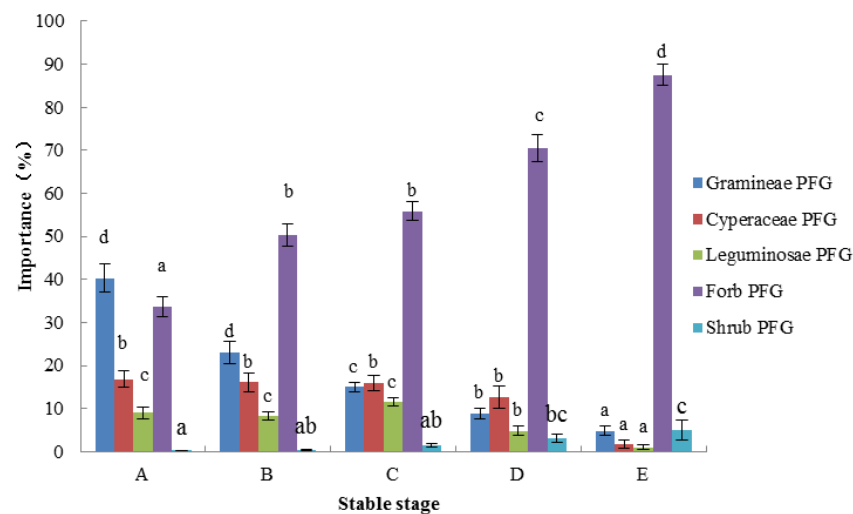


Fig. 2. Importance of plant functional groups in mini-patches at various steady stages

Note: A, B, C, D, and E represent Gramineae–*Kobresia* meadow and Gramineae–*K. humilis* to *K. pygmaea* transitional meadow; healthy and thickening mattic epipedon in *K. pygmaea* meadow; cracking mattic epipedon in *K. pygmaea* meadow; eroded mattic epipedon in *K. pygmaea* meadow and black-soil beach meadow, respectively; a, b, c, d represent significance among different steady stages.

The niche breadths of Gramineae, Cyperaceae, Leguminosae, and forbs decreased as grazing intensity increased. This succession process could also be divided into three periods. The first period was represented by “A” and “B” meadow in which the niche breadths of Gramineae, Cyperaceae, Leguminosae, and forbs were highest among all of the steady stages. The second period was the first regime shift point in which the niche breadth of Gramineae was superseded by the niche breadth of Cyperaceae (see the “C” and “D” steady stages). The third stage was the “E” stage in which the niche breadths of Gramineae, Cyperaceae, Leguminosae, and forbs all greatly decreased. In this process we also found the shrub seemed to increase with grazing intensity increasing, that was not because the steady stage underwent to the shrub meadows,

just because the shrub which always used as the summer pasture had more severe degree degeneration than the alpine meadow used as the winter pasture (Fig. 3).

Overall, our findings showed that the steady stage of alpine meadows maintained the highest plant community primary production relatively constantly under no grazing intensity and under light grazing intensity. When alpine meadows were disturbed by a high grazing intensity, their total yield remained stable but the coefficient of variation in yields increased, which may indicate that change the structure of the plant community changed under these conditions to maintain a steady total biomass.

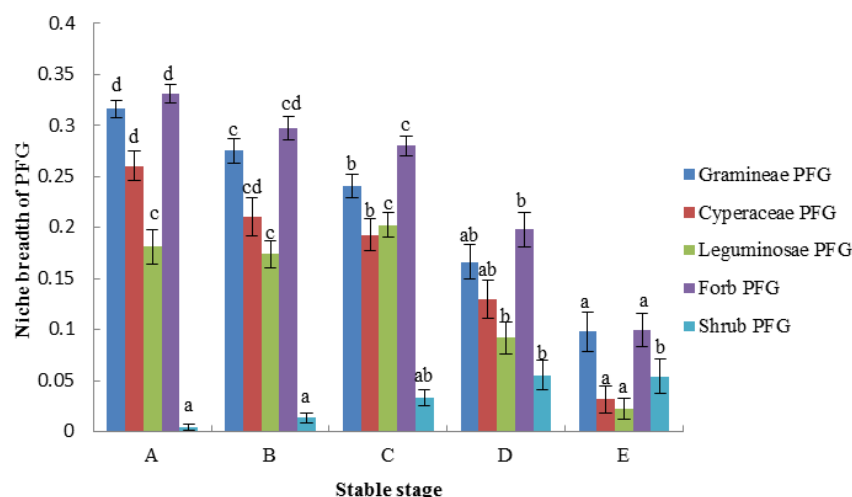


Fig 3. Aboveground niche breadth of functional groups in multi-steady stages

Note: A, B, C, D, and E represent Gramineae–*Kobresia* meadow and Gramineae–*K. humilis* to *K. pygmaea* transitional meadow; healthy and thickening mattic epipedon in *K. pygmaea* meadow; cracking mattic epipedon in *K. pygmaea* meadow; eroded mattic epipedon in *K. pygmaea* meadow and black-soil beach meadow, respectively; a, b, c, d represent significance among different steady stages.

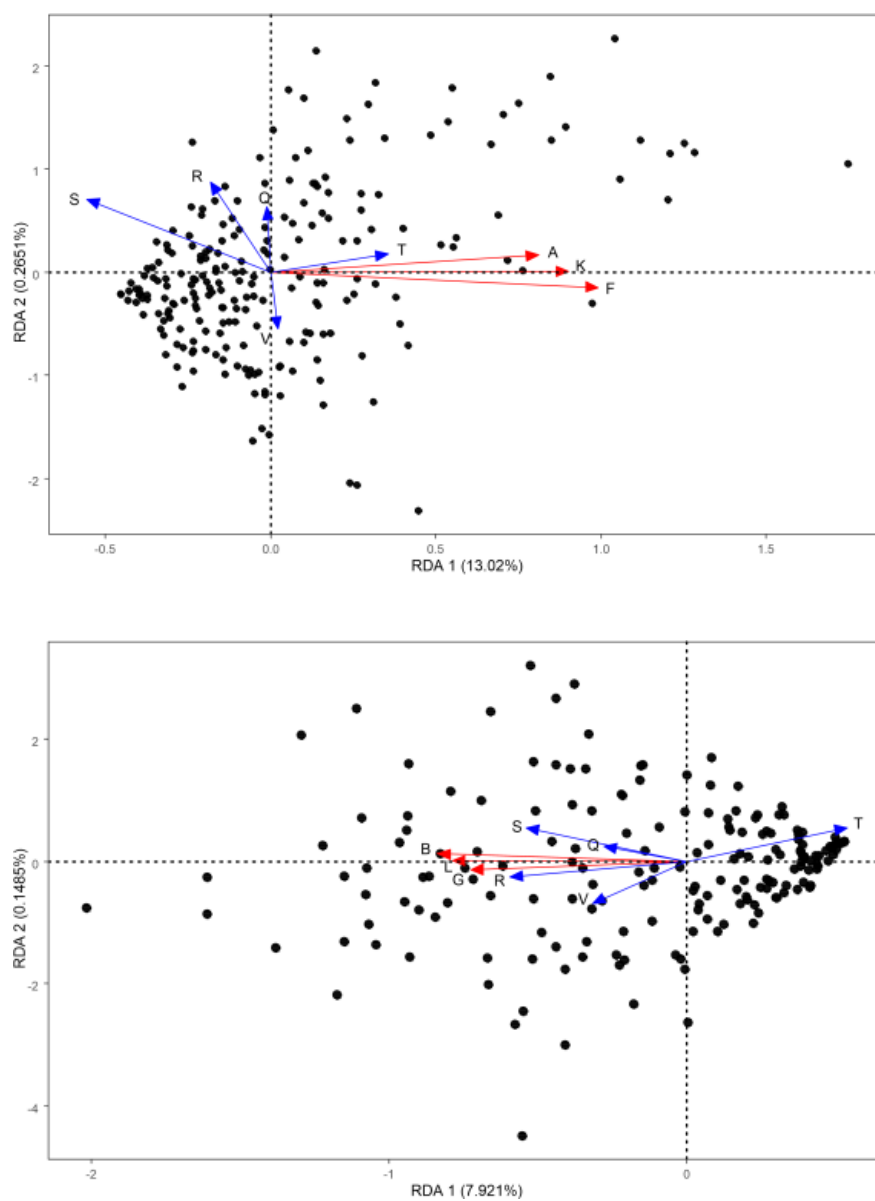
2.2 Effects of geographical location and climatic factors on the formation characteristics of mini-patches in alpine meadow

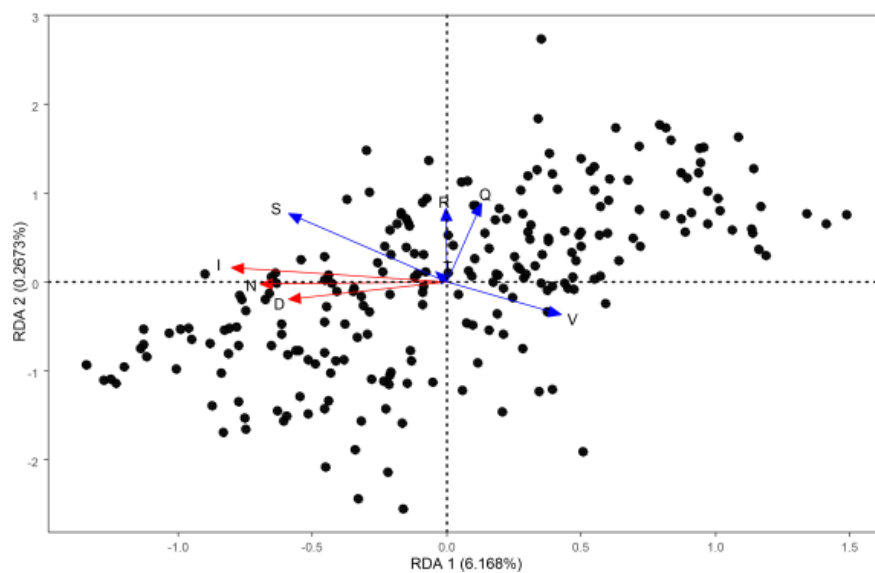
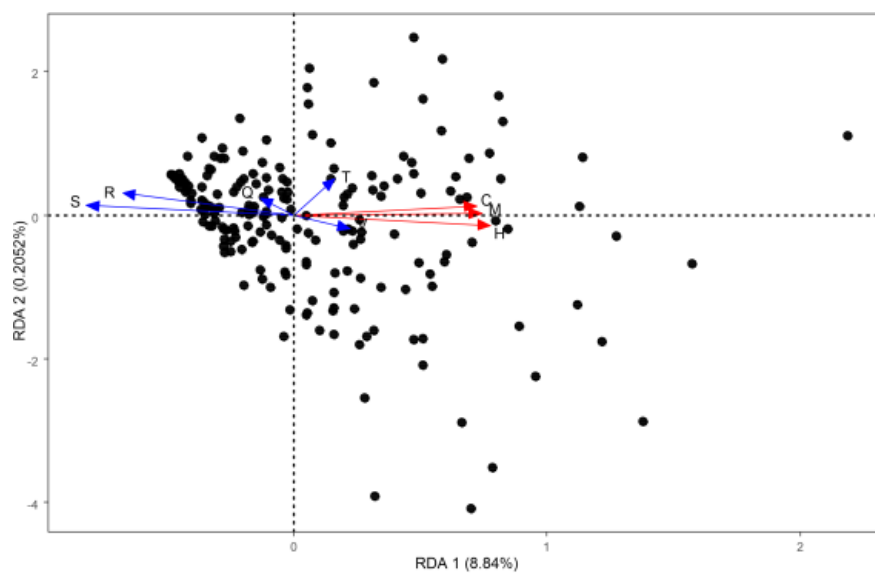
The RDA revealed that the independent variation of latitude, longitude, altitude, accumulated temperature above 0 °C, and accumulation of precipitation explained 13.29%, 8.07%, 9.05%, 6.44%, and 2.44% of the variation in the biomass distribution in mini-patches of Gramineae, Cyperaceae, Leguminosae, forb and shrubs, respectively. With regard to independent variation, there were significant correlations ($P < 0.01$) between geographical location (longitude and latitude) and the characteristics of Gramineae, the accumulation of growing-season precipitation, and altitude and the characteristics of Cyperaceae, the accumulation of growing-season precipitation and longitude and the characteristics of Leguminosae, the accumulation of growing-season precipitation and altitude and the characteristics of forbs, and longitude and the characteristics of shrubs (Fig. 4).

As independent variation explained less than 20% of the total variation in the plant functional groups in mini-patches, environmental factors (latitude, longitude, altitude, accumulated temperature above 0°C, and accumulation of precipitation in growing season) were considered to have no power to explain the variation in the plant functional group distributions (Fig. 4).

The results also revealed that there were no significant correlations between plant community characteristics in mini-patches and geographical location, rainfall, and accumulated temperature characteristics. This sug-

gests that geographical location and climatic characteristics were not the primary drivers of differences in plant community organization and structure in our study area (Fig. 4).





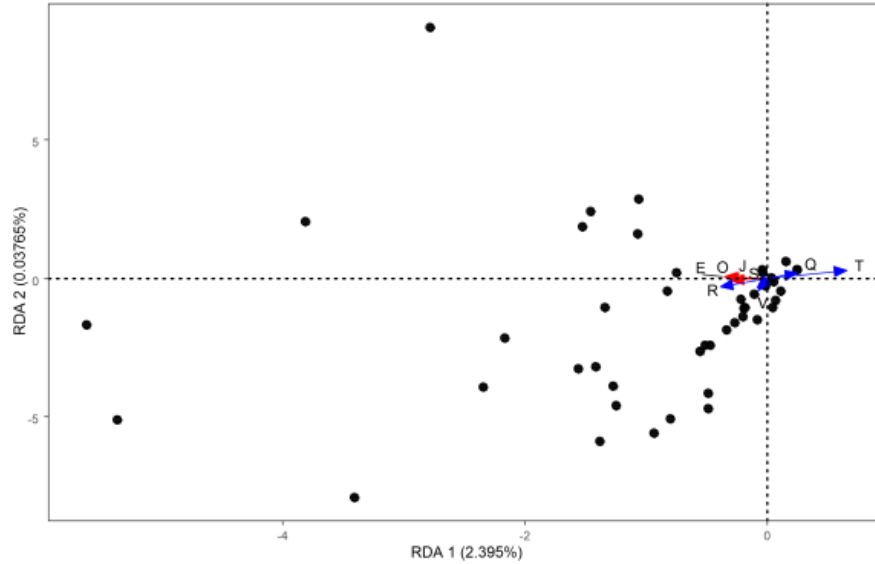


Fig 4. Correlations between plant functional groups and micro-topography and climate

Note: A, F, and K represent the biomass, coverage, and importance value of Gramineae, respectively; B, G, and L represent the biomass, coverage, and importance value of Cyperaceae, respectively; C, H, and M represent the biomass, coverage, and importance value of Leguminosae, respectively; D, I, and N represent the biomass, coverage, and importance value of forbs, respectively; E, J, and O represent the biomass, coverage, and importance values of shrubs, respectively; and P, Q, R, S, and T represent the accumulated temperature above 0°C, the accumulation of precipitation, and latitude, longitude, and altitude, respectively.

2.3 Relationships between micro-topographic factors and steady stages

The characteristics of mini-patches investigated in our research show that 11.1% could be classified to Gramineae–*K. humilis* and Gramineae–*K. humilis* to *K. pygmaea* transitional mini-patches, 16.3% could be classified to healthy and thickening mattic epipedon in *K. pygmaea* meadow, 36.2% could be classified to cracking mattic epipedon in *K. pygmaea* meadow, 16.6% could be classified to eroded mattic epipedon in *K. pygmaea* meadow, and 19.8% could be classified to black-soil beach meadow (Table 2).

Most of the mini-patches were located on sunny or semi-sunny slopes with angles of less than 10° or in valleys between hills. Livestock grazing intensities affected mini-patches differently and the *K. pygmaea* mini-patches were more degraded if they were located in the middle of slopes than if they were located elsewhere. Herders typically use pastures located lower on slopes or in valleys as reserve forage production areas because their superior climate conditions facilitate the growth of forage for use in cases of natural disasters or other emergencies. Therefore, more than 90 % of the Gramineae and Gramineae–*K. humilis* mini-patches occurred in such areas (Table 2).

Our findings indicate that as grazing intensity increased, total plant community coverage decreased. In addition, the total plant community coverage in eroded mattic epipedon *K. pygmaea* meadows and black-soil beach meadows were not significantly different but were lower than that in other types of meadow. In addition, our findings confirm the generally accepted belief that healthy alpine meadows invariably maintain a certain thickness of mattic epipedon (typically 4-5 cm) (Table 2).

Table 2. Micromorphology in alpine meadows under different grazing intensities

	Degree	Proportion of Gramineae– <i>K. humilis</i> (%)	Proportion of Gramineae– <i>K. humilis</i> (%)
Grazing intensity (sheep / ha)	No grazing for more than 1 year	39.5	0.0

	Degree	Proportion of Gramineae- <i>K. humilis</i> (%)	Proportion of <i>K. humilis</i> (%)
Total plant community coverage (%)	< 3.65	60.5	0.0
	3.65–7.5	39.5	14.3
	8.25–13	0.0	53.6
	> 13	0.0	32.1
	> 90	100.0	24.9
	70–90	0.0	16.1
	45–70	0.0	25.0
	< 45	0.0	16.1
Slope aspect	Sunny	66.7	23.8
	Semi-sunny	33.3	76.2
Slope location	Top	0.0	23.8
	Middle	33.3	76.2
	Bottom	66.7	0.0
Slope angle	< 5°	86.8	48.4
	5°–10°	13.2	9.7
	10°–35°	0.0	25.8
	>35°	0.0	16.1
Mattic epipedon thickness (cm)	< 5	73.7	46.4
	5–10	26.3	53.6
	10–13	0.0	0.0
	> 13	0.0	0.0

3 Discussion

3.1 Alpine meadow multi-steady-stage coexistence is a response and adaptation to grazing disturbance under harsh environmental conditions and is mainly controlled by grazing intensity

3.1.1 Alpine meadows are characterized by their long grazing history and extremely fragile environments

Kobresia evolves approximately 240 million years (Shen et al., 2008; Herzsuh, 2006) and alpine meadow soil began forming on the Qinghai-Tibet Plateau 4 ka BP as aeolian dust rapidly accumulated in the Late Holocene and alluvial sediment parent material formed during the middle Holocene (~7–5 ka BP) (Zhang, 2019). Livestock grazing has been performed for approximately 7,300 years (Simons & Schön, 1998; Simons et al., 1994; Georg et al., 2009) and large-scale livestock husbandry for approximately 3,600 years (Qiang et al., 2016). Consequently, alpine *Kobresia* meadow has a long history of livestock grazing, during which both the climate and population densities have fluctuated (e.g., there was a large population during the 6 AD) (Liao & Sun, 2003). Thus, alpine meadows on the Qinghai-Tibet Plateau have the ability to remain stable and recover after repeated disturbances.

3.1.2 Multi-steady stage coexistence is a strategy to resist the adverse effects of disturbance in a harsh environment

Many studies have shown that the degradation succession process in alpine meadows is a typical jump succession process (e.g., Liu et al., 1999). Variations in livestock grazing intensities, particularly those resulting from the household contract system, can change the characteristics (i.e., coverage, height, leave area index) of plant communities and the strategy or nature of plant community organization in response to disturbances (Zhang, 1990).

Most alpine meadow plants (e.g., *K. pygmaea* or *K. humilis*) propagate asexually (Zhou et al., 1986). In the current study, it was found that the density of tillers, leaves, and young shoots increased with a light grazing intensity, this is because the colonization of the asexual branches begins from the outermost leaf layer and

the spacing between the propagule shortened with increasing grazing intensity, and the root-soil ratio (R/S) decreases rapidly, accelerating the imbalance of limiting nutrient in soil supplying and the plant growth demanding, especially in its asexual branches core area (Cao et al., 2010), which leads those branches dead and to emerge bare mini-patches in the centers of *K. pygmaea* patches in heavy grazing intensity *K.pygmaea* or *K. humilis* meadows (Fig. 5).

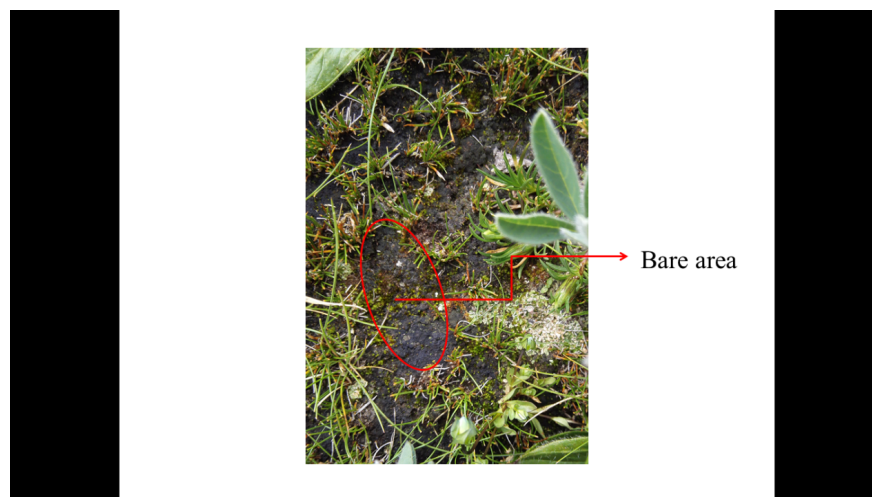


Fig. 5. Bare area (indicated by the red ellipse) in the propagule of *K. pygmaea*

As the ratio between aboveground and belowground biomass decreases with livestock grazing intensity (Cao et al., 2010), grazing can also stimulate root production, increase soil compactness (Fan et al., 2020), decrease water infiltration (Dai et al., 2019), increase the density of dead roots in the core areas of mini-patches, and expand the area of bare mini-patches (Lin, 2017). Thus, the aforementioned asexual reproductive strategy of the dominant species can lead to two results under increasing grazing intensity: increase in bare areas, and the internodes becoming even shorter as the mattic epipedon further thickens (Zhu, 2002).

In alpine *Kobresia* meadows, the formation of mattic epipedon is an adaptive response to livestock trampling and grazing disturbance (Hou et al., 2004). The thickening of mattic epipedon due to overgrazing can affect soil nutrient and water availability and thus change the growth and composition of the plant community. For example, as the niche of Gramineae-type plants (including Gramineae and Cyperaceae functional groups) narrows, the resulting empty resource spaces can be occupied by poisonous or inedible plants that are resistant to trampling and grazing (Lin, 2017). In this manner, the vegetation could maintain high productivity during the growing period and reduced the utility of the pasture for livestock production. This strategy allows a damaged alpine meadow to recover its functional ecology via a new succession process and thereby to adapt to overgrazing. Prior research calculated that it would take 70–80 years for black-soil beach-type grassland to recovery to *K. pygmaea* meadow in an area with no grazing (Chen, 2016).

An alpine meadow could also maintain relatively stable productivity when Gramineae had been reduced as the remaining resources were used by subdominant, poisonous, and inedible species, particularly in heavily disturbed ecosystems. This leads to different plant communities forming in the same topographic and climatic environment and ultimately large-scale multi-stable coexistence (Cao et al., 2007). Therefore, the degradation of alpine meadows to areas with lower edible grass productivity is also a self-regulating process that prevents the occurrence of heavy disturbances.

K. pygmaea meadows occur across a wide region of the Qinghai-Tibet Plateau and can tolerate substantial livestock grazing intensity. This characteristic was dependent on the steady condition maintained by

Cyperaceae plant functional groups, without which these meadows lost their utility for livestock grazing. Therefore, *K. pygmaea* meadows were considered the last line of defense against alpine meadow degradation and were the key to improving alpine meadow productivity.

3.2 Mini-patch patterns in alpine meadows might drive multi-steady stage coexistence

The characteristics of different mini-patches in alpine meadow ecosystems were isolated in space and yet related in function, which imbued ecosystems with a self-organization ability that enabled them to maintain overall stability while permitting small-scale variability. The mini-patches of plant communities in alpine meadows are typically clustered (Zhang et al., 2003), which results in the formation of mosaics of patches in which each patch reflects a certain micro-topography and micro-climate. According to island biogeography theory, mini-patches can be thought of as “islands” and the surrounding areas can be thought as “ocean” (MacArthur & Wilson, 1967). The stability of this plant mosaic system depends on the species turnover rate, patch area, and distance between patches (Bueno & Peres, 2019). While grazing is invariably disturbs to alpine meadow ecosystems, its effect on their patch mosaics is non-homogeneous, which facilitates habitat fragmentation (Jessica et al., 2017). The plant mosaic system therefore resulted in the formation of many types of plant communities with a range of characteristics at different stages during the degradation succession process, with these communities serving as the natural germplasm necessary for the recovery of damaged meadows. Moreover, the interrelationships and permeability of the mosaic patch system in alpine meadows can promote small-scale variability while maintaining system in large-scale stability (Zhang et al., 2003).

The characteristics of alpine *Kobresia* meadows did not appear continuously in multi-steady stages because of the positive and negative feedback effects between various ecosystem components. However, the alpine meadow system is an open system with the ability to self-regulate in response to external disturbances, which is generally manifested as a discontinuous effect in the feedback of external disturbances. This nonlinear superposition effect typically causes a lag around an equilibrium point or critical value in the response of alpine ecosystems to disturbances (Liu et al., 1999). In addition, at a certain critical value in the density of matrix media between mini-patches, infiltration and transformation occurs that drives the plant community into new stages (Oborny & Hubai, 2014). This means that the grazing disturbance pressure of the grassland ecosystem could show a gradual and continuous change process, but the point that leads to the regime shift among different steady stages discontinuous, that is, only when the grazing pressure reached a critical value, the regime shift should be occurred, so succession process among different steady stages of alpine meadows was sudden change, not gradual change.

Alpine meadows have high plant diversity compared to most plant communities growing in dry and cold regions, and this is also true for mini-patches. Therefore, the degree of degradation of alpine meadows was best estimated by determining the frequency or pattern of mini-patches rather than their overall richness in plant community species.

Human factors have played important role in changing alpine ecosystems and resources in China over the past 70 years (Yang et al., 2016). The basic cause of alpine meadow degradation at small spatiotemporal scales is unsustainable human exploitation, and intense pasture use inevitably leads to degradation and subsequent reduction in regional economic and social services (Wang, 2004). Secondary effects such as rodent gnawing and digging are not initial causes of degradation but arise from the degradation caused by overgrazing (Zhang & Fan, 2002). Thus, while estimating the service function of alpine meadows improves understanding of mini-patch patterns on such meadows, the substantial problem of managing the degradation of alpine meadows remains.

References

- Bueno, S.A., Peres, A.C. (2019). Patch-scale biodiversity retention in fragmented landscapes: Reconciling the habitat amount hypothesis with the land biogeography theory. *Journal of Biogeography*, 46(3), 621-632.
- Cao, G. M., Du, Y. G., Liang, D. Y., Wang, Q. L., Wang CH. T. (2007). Character of passive-active degradation process and its mechanism in alpine *Kobresia* meadow. *Journal of Mountain Science*, 25(6),

641-648.

- Cao, G. M., Long, R. J., Zhang, F. W., Li, Y. K., Lin, L., Guo, X. W., Han, D. R., Li, J. (2010). A method to estimate carbon storage potential in alpine Kobresia meadows on the Qinghai-Tibetan Plateau. *Acta Ecologica Sinica* , 30 (23), 6591-6597.
- Chen, W. (2016). Succession characteristics of *Kobresia pygmaea* plaques in artificial grassland of black soil beach. *Qinghai University* , Xining, China.
- Dai, L., Guo, X. W., Zhang, F. W., Du, Y. G. Ke, X., Li, Y. N., Cao, G. M., Li, Q. Lin, L., Su, K. (2019). Seasonal dynamics and controls of deep soil water infiltration in the seasonally frozen region of the Qinghai-Tibet plateau. *Journal of Hydrology* , 571, 740-748.
- Fan, B., Lin, L., Cao, G. M., Li, Y. K., Pengcuo, J., Du, Y. G., Guo, X.W., Li Q., Qian, D. W. (2020). Relationship between plant roots and physical soil properties in alpine meadows at different degradation stages. *Acta Ecologica Sinica* , 40(7), 300-2309.
- Gonzalez, M., Ladet, S., Deconchat, M., Cabanettes, A., Alard, D., Balent, G. (2010). Relative contribution of edge and interior zones to patch size effect on species richness: An example for woody plants. *Forest Ecology and Management* , 259(3), 266-274.
- Herzschuh, U. (2006). Palaeo-moisture evolution at the margins of the Asian monsoon during the last 50,000 years. *Quaternary Science Reviews* , 25(1-2), 163-178.
- Hou, F. J., Chang. SH. H., Yu, Y. W., Lin H. L. (2004). A review on trampling by grazed livestock. *Acta Ecologica Sinica* , 24(4), 784-789.
- Jessica, Z. M., Garry, R. R., Rene, A. A., Abner, A. B., Sean, R. C. (2017). Network theory and metapopulation persistence: Incorporating node self-connections. *Ecology Letters* , 20(7), 815-831. doi:10.1111/ele.12784.
- Jørgensen, E. S., Nielsen, N. S., Fath, D. B. (2016). Recent progress in systems ecology. *Ecological Modelling* , 319, 112-118.
- Klinerová, T., Dostal, P. (2020). Nutrient-demanding species face less negative competition and plant-soil feedback effects in a nutrient-rich environment. *New Phytologist*, 225(3), 1343-1354.
- Lauren, M. S. R. (2018). Predators in the plant-soil feedback loop: Aboveground plant associated predators may alter the outcome of plant-soil interactions. *Ecology Letters* , 21(5), 646-654.
- Liao, S., Sun, J. (2003). GIS-based spatialization of population census data in Qinghai-Tibet Plateau. *Acta Geographica Sinica*, 58(1), 25-33.
- Lin, L. (2017). Response and adaptation of plant-soil system of alpine meadows in different successional stages to grazing intensity. *Gansu Agricultural University* , Lanzhou, China.
- Liu, W., Wang, Q. L., Wang, X., Zhou, L., Li, F. J. (1999). Ecological process of forming “black-soil-type” degraded grassland. *Acta Agrestia Sinica* , 7(4), 300-307
- MacArthur, R., Wilson, E. (1967). The theory of biogeography. *Princeton University Press* , Princeton, USA, 19-67.
- Meng, F. D., Wang, S. H., Bai, L. (2014) The climate change and alpine grassland on the Tibetan Plateau. *Guihaia* , 34(2), 269-275.
- Miehe, G., Miehe, S., Schlütz, F. (2009). Early human impact in the forest ecotone of southern High Asia (Hindu Kush, Himalaya). *Quaternary Research* , 71 (3), 255-265.
- Koper, N., Mozel, E. K., Henderson, C. D. (2010). Recent declines in northern tall-grass prairies and effects of patch structure on community persistence. *Biological Conservation* , 143(1), 220-229.

- Oborny, B., Hubai, G. A. (2014). Patch size and distance: modelling habitat structure from the perspective of clonal growth. *Annals of Botany* , 114(2), 389-398.
- Proulx, M., Mazumder, A. (1998). Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* , 79 (8), 2581-2592.
- Qiu, Q., Wang, L., Wang, K., Yang, Y. ZH., Ma, T., Wang, Z. F., Zhang, X., Ni, ZH. Q., Hou, F. J., Long, R. J., Abbott, R., Lenstra, J., Liu, J. Q. (2016). Yak whole-genome resequencing reveals domestication signatures and prehistoric population expansions. *Nature Communications* , 6: 10283.
- Shen, C., Liu, K. B., Morrill, C., Overpeck, J., Peng J., Tang L. (2008). Ecotone shift and major droughts during the mid-late Holocene in the central Tibetan Plateau. *Ecology* , 89(4), 1079-1088.
- Simons, A., Schön W. (1998). Cave systems and terrace settlements in Mustang, Nepal: Settlement periods from prehistoric times up to the present day. *Beiträge zur Allgemeinen Vergleichenden Archäologie* , 18, 27-47.
- Simons, A., Schön, W., Shrestha, S. S. (1994). Preliminary report on the 1992 campaign of the team of the Institute of Prehistory, *University of Cologne* , Ancient Nepal, 136, 51-75.
- Wang, SH. P. (2004). Grazing resistance of rangeland plants . *Chinese Journal of Applied ecology* , 15(3), 517-522.
- Wedin, D. A., Tilman, D. (1996). Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science* , 274(5293), 1720-1723.
- Wellemeyer, C. J., Perkin, S. J., Jameson, L. M., Costigan, K. H., Waters, R. (2019). Hierarchy theory reveals multi-scale predictors of Arkansas darter (*Etheostoma cragini*) abundance in a Great Plains riverscape. *Freshwater Biology* , 64(4), 659-670.
- Wu Y, Wen T, Huo G, Lü J. ZH., Li, H. SH., Hu G. W. (2012). Micro-scale spatial heterogeneity of vegetation community and soil organic matter under different grazing intensities. *Journal of Desert Research* , 32(4), 972-979.
- Xu P. (1994). Grassland resources investigation and planning. *China Agricultural Press* , Beijing ,China.
- Yang, L., Han, M., Li, J. (2001). Plant diversity change in grassland communities along a grazing disturbance gradient in the northeast China transect. *Acta Phytocologica Sinica*, 25(1), 110-114.
- Yang, R. R. (2002). The causes and sustainable development of grassland degradation in Western China. *Pratacultural Science* , 19(1), 23-27.
- Yang, ZH. L., Yuan, G. J., Zhou, L. (2016). Grassland management and sustainable development strategy in grassland husbandry industry. *Rural Economy & Technology* , 27(24), 29.
- Zhang, J. (2019). Study of forming-chronology and its climatic background of alpine meadow soil in the Qinghai Lake basin. *Qinghai Normal University* , Xining, China
- Zhang, J. X., Cao, G. M., Zhou, D. R., Hu, Q. W., Zhao, X. Q. (2003). The carbon storage and carbon cycle among the atmosphere, soil, vegetation and animals in the *Kobresia humilis* alpine meadow ecosystem. *Acta Ecologica Sinica* , 23(4), 627-634.
- Zhang, W. G., Huang, W. B., Yang, Z. Y. (2003). The study on the relationship between mini-patch and degradation of pasture. *Acta Prataculturae Sinica* , 12(3), 44-50.
- Zhang, Y. (1990). A quantitative study on characteristics and succession pattern of alpine shrub lands under different grazing intensities. *Acta Phytocologica Sinica* , 14(4), 358-365.
- Zhong, W. Q., Fan, N. CH. (2002). The causes of rat infestation in China grassland and the countermeasures of ecological control. *Biology Bulletin* , 37(7), 1-5.

Zhu, ZH. H. (2002). Studies on the structural hierarchy and the functional hierarchy in clonal plants: with example of *Kobresia humilis* , *Lanzhou University* , Lanzhou, China.

Zhou, X., Wang, Z., Du, Q. (1986). Qinghai vegetation. *Qinghai People's Publishing House* , Xining, China.