Disturbance of plateau zokor-made mound stimulates plant community regeneration in the Qinghai-Tibetan Plateau, China postprint

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Abstract

Mounds constructed by plateau zokors, which are widely distributed in alpine meadows, significantly modify plant community structure. However, variations in plant community structure under the disturbance of zokor-made mounds have received limited attention. Therefore, we investigated plant community responses on zokor-made mounds of different ages (1 year and 3–4 years) and compared them with undisturbed sites (no mounds) in an alpine meadow in the eastern Qinghai-Tibetan Plateau (QTP), China. Species richness, coverage, and Simpson diversity index were all significantly reduced by the presence of zokor-made mounds, whereas plant heights were significantly increased, particularly in grasses and sedges. Several perennial forage species exhibited increased importance values and niche breadth, including *Koeleria macrantha*, *Elymus nutans*, and *Poa pratensis*. The effect of zokor-made mounds on niche overlap indicated that more intense interspecific competition led to greater utilization of environmental resources. This interspecific niche overlap intensified as succession progressed. The bare mounds created by zokor burrowing activities provided colonization opportunities for non-dominant forage species, resulting in high species richness and plant diversity during the succession period. We conclude that the presence of zokor-made mounds promotes regeneration and vitality of plant communities in alpine meadows, thereby enhancing their resilience to anthropogenic stress.

Full Text

Disturbance by Plateau Zokor-Made Mounds Stimulates Plant Community Regeneration in the Qinghai-Tibetan Plateau, China

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Abstract: Mounds constructed by plateau zokors significantly modify plant community structure, yet variations in community structure under zokor disturbance have received limited attention. We investigated plant community responses on zokor-made mounds of different ages (1 year and 3–4 years) and compared them with undisturbed sites (no mound) in an alpine meadow in the eastern Qinghai-Tibetan Plateau (QTP), China. Species richness, coverage, and Simpson diversity index were all significantly reduced by the presence of zokor-made mounds, while plant heights increased significantly, particularly in grasses and sedges. Several perennial forage species showed increased importance values and niche breadth, including *Koeleria macrantha*, *Elymus nutans*, and *Poa pratensis*. Analysis of interspecific niche competition revealed greater utilization overlap, indicating more efficient use of environmental resources, and this interspecific niche overlap strengthened as succession progressed.

The bare mounds created by zokor burrowing activities provided colonization opportunities for non-dominant forage species, resulting in abundant plant species and enhanced diversity during the succession period. We conclude that the presence of zokor-made mounds is conducive to regeneration and vitality of plant communities in alpine meadows, thus improving their resilience to intense anthropogenic stress.

Keywords: rodent; mound; zokor disturbance; alpine meadow; vegetation recovery; niche

1 Introduction

The Qinghai-Tibetan Plateau (QTP) in China is the world' s largest alpine pastoral ecosystem, providing ecological benefits including carbon sequestration, soil and water conservation, aesthetic recreation and tourism, and economic benefits from pastoral production (Feng et al., 2010; Wang et al., 2016; Hopping et al., 2018; Zhang et al., 2019; Dong et al., 2020; Liu et al., 2020). However, these meadows are threatened by increased livestock grazing and human population growth (Harris, 2010; Nyima, 2017), as well as a changing climate that

is thawing permafrost and facilitating population growth of burrowing rodents (Xue et al., 2009; Harris, 2010; Xue et al., 2017), resulting in varying degrees of degradation. Alpine meadow degradation threatens pastoral livelihoods and ecological function through soil erosion and nutrient loss (Li et al., 2013; Lu et al., 2017; Liu et al., 2018; Wang et al., 2020; Yuan et al., 2020).

The plateau zokor (*Myospalax baileyi*) is a subterranean rodent endemic to alpine meadows of the QTP (Wang et al., 2008; Hu et al., 2017). This species is often described as a major pest because its foraging, digging, and mound-making activities produce highly visible changes to the meadow landscape, and its impacts on plant diversity, biomass, soil organic carbon, temperature, and soil water holding capacity are usually characterized as negative (Wang et al., 2008; Li et al., 2009; Zhang et al., 2014; Hu et al., 2017; Chu et al., 2020). Enzyme activity and microbial biomass are lower in zokor-made mounds than in surrounding undisturbed soil (Li et al., 2009). Nevertheless, recent studies have suggested positive ecological benefits of plateau zokors, including increased soil water availability, soil organic carbon, and diverse plant communities across the meadow (Wang et al., 2008; Wu et al., 2017). Both seed germination and seedling survival are higher on zokor-made mounds (Bao et al., 2016; Hu et al., 2017), and moderate habitat disturbance by plateau zokors may stimulate species recruitment and increase meadow plant diversity, thereby improving regeneration after overgrazing (Wu et al., 2015; Hu et al., 2017).

Few studies have examined niche characteristics of plant communities in alpine meadows disturbed by plateau zokors (Hu et al., 2017). To address this gap, we studied plant community structure on zokor-made mounds of different ages. Our aims were to: (1) characterize plant community succession after disturbance by mound construction in meadows; (2) determine the responses of niche characteristics of plant communities to mound construction; and (3) compare the effects of zokor-made mounds on the recovery of plant diversity.

2.1 Study Area

The research area was located at the Hongyuan County Alpine Meadow Ecosystem Research Station of Southwest Minzu University, China. Hongyuan County lies on the eastern margin of the QTP (31°50 -33°22 N, 101°51 -103°23 E). Annual precipitation is 650–730 mm, falling mostly between May and August. The average altitude is 3500 m a.s.l., the annual mean temperature is 1.1°C, and the mean annual duration of snow cover is 76 days (Li et al., 2011).

2.2 Sampling and Measurements

Plant coverage, height, and frequency were recorded for each species in nine replicate plots across three mound treatments in September 2011. Treatments included undisturbed meadow control (no mound), and zokor-made mounds aged one year (1 a) and three to four years (3–4 a) since construction, with plots selected randomly from the meadow. Mounds had been abandoned by

zokors at the time of study. The 1 a mound was constructed in August 2010, and at the time of study had a surface area of 0.6 m^2 and a height of 80–100 mm. The 3–4 a mound was constructed on or before 2008, and at the time of study had a surface area of 0.4 m^2 and a height of 30–50 mm. Control plots of 1.0 m^2 were selected on sites showing no visible signs of mound construction. Plant species were classified into four functional groups for further analysis: grass, sedge, legume, and forb (Hu et al., 2017).

2.3 Data Analysis

Importance value (IV) of each species was calculated using the following equation:

$$IV = (Cr + Hr + Fr)/3,$$

where Cr, Hr, and Fr are relative coverage, relative height, and relative frequency, respectively (Hu et al., 2017).

Three diversity indices were calculated: Shannon–Wiener diversity index (H), Simpson diversity index (D; Lande, 1996), and Pielou evenness index (E; Pielou, 1966). The calculation formulas are given below:

$$H = -\sum_{i=1}^{S} P_i \ln P_i,$$

$$D = \sum_{i=1}^{S} P_i^2,$$

$$E = H/\ln S,$$

where P_i is the importance value and S is plant species richness (Fang et al., 2009).

Six indices were used to assess niche characteristics of plant communities: (1) Levins niche breadth index (NBL; Hurlbert, 1978); (2) Shannon–Wiener niche breadth index (NBSW; Colwell and Futuyma, 1971); (3) Hurlbert niche breadth index (NBH; Hurlbert, 1978); (4) Levins coefficient of niche overlap (Oik; Hurlbert, 1978); (5) ecological attributes (ΔOik); and (6) ecological response rate (R; Zhang, 2018). The equations are given below:

$$NBL = 1/\sum_{j=1}^{n} P_{ij}^2,$$

$$NBSW = -\sum_{j=1}^{n} P_{ij} \ln P_{ij},$$

$$NBH = (nNBL - 1)/(n - 1),$$

$$Oik = \sum_{j=1}^{n} P_{ij} P_{kj},$$

$$\Delta Oik = Oik - Oki,$$

$$R = NB/\Delta Oik \quad (i = k),$$

where $P_{ij} = n_{ij}/N_i$; n_{ij} is the dominance of the ith population in the jth resource state; P_{ij} is the proportion of dominance of the ith population in the jth resource state to the total dominance of the ith population in all resource states; n is the number of resource states; P_{kj} is the proportion of dominance of the kth population in the jth resource state to the total dominance of the kth population in all resource states; Oik is the amount of resources occupied by population k due to population i; Oki is the amount of resources occupied by population i due to population k. If $Oik > Oki$, population i is developmental; otherwise, population k is declining; and NB is the niche breadth of plant species. The total niche overlap value equals the niche overlap value of all species pairs divided by the total number of species pairs in the plant community.

All data were checked for normality and homogeneity of variance. Normality was tested using the Kolmogorov-Smirnov Z method ($P < 0.05$) in a nonparametric test. Homogeneity of variance was tested using the Levene test ($P < 0.05$). One-way analysis of variance (ANOVA) with Bonferroni' s multiple range test ($P < 0.05$) was performed to assess the effects of different zokor-made mound types (1 a, 3–4 a, and no mound) on plant species richness, height, H, E, and plant functional groups, which met assumptions of normality and homogeneity of variance. Data that failed these assumptions for parametric testing were analyzed using the nonparametric Kruskal-Wallis H test ($P < 0.05$). Oik and Oki of plant species in the community were compared using the Kruskal-Wallis H method ($P < 0.05$) in the nonparametric test. Differences obtained at the $P < 0.05$ level were considered significant. Niche breadth (NBSW, NBL, and NBH) and ecological response rate (R-NBSW, R-NBL, and R-NBH) of plant species were analyzed by principal component analysis (PCA) in CANOCO 5.0 software (Version 5.0 for Windows; Ter Braak and Smilauer, 2012) to identify changes in niche characteristics among plant communities.

3.1 Characteristics of Plant Community Structure

Zokor-made mounds reduced plant species richness, coverage, and Simpson diversity index, while Shannon–Wiener diversity and Pielou evenness indices were unaffected. Plant height in zokor-made mounds increased significantly (Table 1).

Species richness of sedge and legume decreased significantly compared with no mound, but species richness of grass and forb were unaffected (Fig. 1 [Figure 1: see original paper]). Grass coverage was greater in 3–4 a mounds than in both 1 a and no mound treatments, with the latter two not significantly different. There was no significant difference in sedge coverage, but legume coverage in 1 a mounds was significantly lower. Forb coverage was highest in 1 a mounds and lowest in 3–4 a mounds. Grass heights in both 1 a and 3–4 a mounds were significantly greater than in no mound plots. Sedge height in 3–4 a mounds was greater than in both 1 a and no mound treatments. Legume and forb heights declined in both 1 a and 3–4 a mounds (Fig. 1).

Table 1 Effect of zokor-made mound on plant community structure

Index	Mound type	Statistical result
Species richness	$18.44\$\pm4.50ab(1a), 13.56\pm6.86a(3–4a), 21.56\pm6.93b(nomound)\|F\{2\},\{24\}\$ = 3.81, P < 0.001$	
Coverage (%)	$82.56\$\pm3.17a(1a), 13.48\pm0.72a(3–4a), 91.56\pm4.82b(nomound), 97.44\pm1.33b(nomound)\|H = 20.25, P < 0.001\|\|Height(cm)\|13.50\pm1.08a(1a), 12.43\pm0.69b(3–4a)\|F\{2\},\{24\}\$ = 4.70, P < 0.001$	
Simpson diversity index	$0.958\$\pm0.005a(1a), 0.941\pm0.013a(3–4a), 0.967\pm0.001b(nomound)\|H = 21.08, P < 0.001\|\|Shannon–Wienerdiversityindex\|2.355\pm0.428(1a), 1.906\pm0.623(3–4a), 2.538\pm0.518(no\$ = 3.40, P > 0.05$	
Pielou evenness index	$0.810\$\pm0.080(1a), 0.756\pm0.077(3–4a), 0.831\pm0.084(nomound)\|F\{2\},\{24\}\$ = 2.05, P > 0.05$	

Note: Different lowercase letters within the same row indicate significant differences among mound types at $P < 0.05$ level. H is the statistic value of the nonparametric Kruskal-Wallis H test. Mean±SE.

Fig. 1 Species richness (a–d), coverage (e–h), and height (i–l) for each plant functional group and zokor-made mound type. Different lowercase letters indicate significant differences among mound types at $P < 0.05$ level.

3.2 Niche Breadth of Plant Species

Zokor-made mounds significantly affected the niche breadth of the 41 observed plant species (Table 2). The three formulae (NBSW, NBL, and NBH) produced

different values but similar trends across species (Fig. 2 [Figure 2: see original paper]). Dominant species differed among treatments. The 1 a mound was dominated by grasses (*Koeleria macrantha*, *Elymus nutans*, and *Poa pratensis*) and forbs (*Stellaria infracta*, *Ranunculus tanguticus*, *Artemisia annua*, and *Potentilla anserina*). The 3–4 a mound was also dominated by grasses (*P. pratensis*, *E. nutans*, and *K. macrantha*) and forbs (*S. infracta* and *Lancea tibetica*). However, in no mound plots, forbs (*Anemone rivularis*, *Saussurea nigrescens*, *R. tanguticus*, *P. anserina*, *Anaphalis lactea*, and *Gentiana ornate*), legumes (*Tibetia himalaica* and *Oxytropis ochrocephala*), one grass (*Festuca rubra*), and one sedge (*Carex kansuensis*) were dominant (Table 2).

Table 2 Importance value (IV) and ecological attribute value (ΔOik) for each plant species under different types of zokor-made mound

[Table content with species S1–S41, functional groups, life cycles, and values for 1 a, 3–4 a, and no mound treatments]

Note: S1–S41 indicate plant species. - indicates no value. P, perennial; A, annual.

Fig. 2 Shannon–Wiener niche breadth index (a), Levins niche breadth index (b), and Hurlbert niche breadth index (c) of plant species under different types of zokor-made mound. S1–S41 indicate plant species.

3.3 Niche Overlap of Plant Species

Most species pairs showed niche overlap in 1 a mounds (91.18%; Table S1), 3–4 a mounds (87.19%; Table S2), and 100.00% in no mound plots (Table S3). The proportions of species pairs with niche overlap >0.6, >0.7, >0.8, >0.9, and >1.0 were 51.18%, 40.86%, 30.11%, 20.22%, and 8.17% in 1 a mounds, respectively; 47.41%, 40.52%, 36.21%, 32.76%, and 19.33% in 3–4 a mounds, respectively; and 55.35%, 46.97%, 38.59%, 27.45%, and 9.18% in no mound plots, respectively. Total niche overlap in 1 a mounds, 3–4 a mounds, and no mound plots was 58.32%, 59.31%, and 65.91%, respectively. Niche overlap of plant species was initially small in new zokor-made mounds and increased gradually as succession progressed. The proportions of species pairs in 3–4 a mounds with niche overlap >0.9 and >1.0 were 12.54% and 11.16%, which were 12.54% and 10.62%, and 5.31% and 10.15% higher than those in 1 a mounds and no mound plots, respectively. These results indicate that competition among plant species increases over time, resulting in increased interspecific niche overlap.

3.4 Ecological Response Rate (R) of Plant Species

Based on ΔOik values, we identified 18 developmental and 13 declining populations in 1 a mounds (Table 2). The main developmental populations were *K. macrantha*, *E. nutans*, *R. tanguticus*, *S. infracta*, and *A. annua*, while the main declining populations were *C. periacanthaceum*, *A. fatua*, *T. lugubre*, *G. paludosa*, and *P. nivea*. In 3–4 a mounds, we found 13 developmental and 16

declining populations. The main developmental populations were *P. pratensis*, *S. infracta*, *E. nutans*, and *L. tibetica*, while the main declining populations were *P. anserina*, *P. kansuensis*, *A. lactea*, *H. elliptica*, *D. caeruleum*, *F. rubra*, *A. rivularis*, and *L. nanum*. In no mound plots, we found 17 developmental and 17 declining populations. *A. rivularis*, *S. nigrescens*, *R. tanguticus*, *T. himalaica*, *P. anserina*, *O. ochrocephala*, *F. rubra*, and *A. lactea* were the main developmental populations, while *F. ovina*, *G. abaensis*, *P. pratensis*, *E. nutans*, *S. graminea*, *P. kansuensis*, *T. farreri*, and *G. paludosa* were the main declining populations.

Ecological response rates of different populations to the habitat are represented by R values. Among developmental populations in 1 a mounds, *T. distigmaticum* (R-NBSW = 2.41, R-NBL = 0.86, R-NBH = 0.80), *C. kansuensis* (R-NBSW = 1.13, R-NBL = 0.40, R-NBH = 0.36), and *A. rivularis* (R-NBSW = 1.04, R-NBL = 0.38, R-NBH = 0.35) showed higher R values, whereas *F. rubra* (R-NBSW = -2.35, R-NBL = -0.81, R-NBH = -0.73) was the most declining population with larger negative R values (Fig. 3 [Figure 3: see original paper]). In 3-4 a mounds, *T. himalaica* (R-NBSW = 1.60, R-NBL = 0.49, R-NBH = 0.40) was the main developmental population, while *C. kansuensis* (R-NBSW = -1.97, R-NBL = -0.63, R-NBH = -0.56) and *F. ovina* (R-NBSW = -1.17, R-NBL = -0.38, R-NBH = -0.33) were declining populations (Fig. 3). In no mound plots, *T. distigmaticum* was the main developmental population (R-NBSW = 2.54, R-NBL = 0.88, R-NBH = 0.81), while *L. tibetica* (R-NBSW = -1.82, R-NBL = -0.62, R-NBH = -0.56), *A. tenuifolia* (R-NBSW = -1.71, R-NBL = -0.59, R-NBH = -0.53), and *H. elliptica* (R-NBSW = -1.21, R-NBL = -0.41, R-NBH = -0.37) were the main declining populations (Fig. 3).

Fig. 3 Ecological response rates (R) of plant species under different types of zokor-made mound. R-NBSW, ecological response rate of Shannon–Wiener index (a); R-NBL, ecological response rate of Levins index (b); R-NBH, ecological response rate of Hurlbert index (c). S1–S41 indicate plant species.

3.5 Responses of Niche Breadth and R to Zokor-Made Mounds

PCA ordination of niche breadth and R values showed that the cumulative contribution rates of variance for the two principal components were 86.67% and 89.02%, respectively (Figs. 4 and 5). The three mound types were clearly separated by niche characteristics. *Elymus nutans*, *P. pratensis*, *A. annua*, and *S. infracta* occupied larger areas in new mounds (Fig. 4 [Figure 4: see original paper]). *E. nutans*, *P. pratensis*, *L. nanum*, *S. infracta*, and *E. arvense* were the most sensitive species in 3-4 a mounds, with three of these (*E. nutans*, *P. pratensis*, and *S. infracta*) having larger niche breadth compared with other species. In no mound plots, *F. rubra*, *K. capillifolia*, *O. ochrocephala*, *A. tenuifolia*, *S. graminea*, *L. stracheyi*, *T. lugubre*, *A. rivularis*, *G. leucomelaena*, *G. abaensis*, and *G. ornata* showed higher correlation with habitat compared with other species. Additionally, different plant functional groups such as *F.*

rubra (grass), *K. capillifolia* (sedge), *O. ochrocephala* (herbaceous legume), *A. rivularis* (forb), and *G. ornata* (forb) all occupied larger niche breadth, indicating that the composition of plant functional groups was stable and plant diversity was high in no mound treatment (Fig. 4; Table 2).

PCA ordination of R in 1 a mounds showed that *E. nutans*, *P. pratensis*, *A. annua*, *A. rivularis*, *G. pylzowianum*, *P. depressa*, *T. farreri*, *H. elliptica*, and *S. infracta* were the most sensitive species after disturbance (Fig. 5 [Figure 5: see original paper]). R values of *A. rivularis*, *G. pylzowianum*, *P. depressa*, and *T. farreri* were higher. In 3-4 a mounds, *S. nigrescens*, *P. nivea*, *R. tanguticus*, and *V. eriogyne* had higher R values, making them the most sensitive species (Fig. 5). However, PCA ordination of R in no mound plots showed that *K. macrantha*, *F. rubra*, *K. capillifolia*, *O. ochrocephala*, *A. sikkimense*, *G. leucomelaena*, and *G. ornate* had higher correlation with habitat compared with other species (Fig. 5). Sedge *K. capillifolia* and forb *G. leucomelaena* showed higher R values.

Fig. 4 Principal components analysis (PCA) of niche breadth under different types of zokor-made mound. S1–S41 indicate plant species.

Fig. 5 Principal components analysis (PCA) of ecological response rate under different types of zokor-made mound. S1–S41 indicate plant species.

4 Discussion

Disturbance by burrowing rodents is widespread across ecosystems. In tundra grasslands, rodents positively affect nutrient cycling by modifying nutrient dynamics of plant communities; for example, disturbance increased nutrient content of forbs and grasses (Bon et al., 2020). In arid grasslands, plant community structure differed between mounds and landscape patches occupied by two rodents (*Cynomys gunnisoni* and *Dipodomys spectabilis*), and the rodents increased landscape heterogeneity, plant species richness, and forb coverage (Davidson and Lightfoot, 2008). Similarly, disturbance by rodents (*Rhombomys opimus*, *Cricetulus migratorius*, *Meriones meridianus*, and *Dipus sagitta*) altered morphologies and nutrients of *Haloxylon ammodendron* in deserts, as well as increased soil organic matter, total nitrogen, available nitrogen, and available potassium contents (Xiang et al., 2020). However, disturbance by rodents (*Ctenomys mendocinus*) reduced plant coverage, diversity, and density (Lara et al., 2007). In tallgrass prairie, selective foraging on two legumes and one coneflower by voles altered plant community structure and reduced plant diversity (Howe and Brown, 1999). In grasslands, rodent disturbance reduced productivity (Maron et al., 2014). Based on these studies, we believe that rodent disturbance has both positive and negative effects on plant communities in alpine meadows. The plateau zokor, a typical alpine meadow rodent, plays an important role in ecosystem functions such as soil nutrient cycling and soil structure, creating heterogeneous habitat patches and functioning as an ecosystem engineer (Zhang and Liu, 2003). Mound-making by plateau zokors is an important determinant of plant community composition in alpine meadows (Hu

et al., 2017); however, how zokor-made mound disturbance affects niche characteristics of plant communities in alpine meadows has often been ignored.

Niche breadth can be used as an indicator to measure the scale of species' utilization of environments or resources. Usually, species with higher importance values can use more resources or tolerate variable environmental conditions and distribute more widely, resulting in larger niches (Dostál et al., 2016; Pannek et al., 2016). The larger the niche breadth of a species, the more completely environments or resources are utilized, and the larger the species' habitat range (Sheth et al., 2020). Species differ in their competitive abilities to use habitat resources, affecting their niche breadths. In an ecosystem, heterogeneous habitat created by the original community after disturbance causes release of niche space, and species then affect community structure by competing for or preempting niche space in heterogeneous habitat (Yang et al., 2018). Generally, because each species has equal competitive opportunity to colonize bare zokor-made mounds and occupy niches during succession, different types of forages can coexist, resulting in more abundant plant species in the climax community.

Our study yielded similar results to Yang et al. (2018) and Niu et al. (2020), in that composition characteristics of plant communities differed at earlier stages of succession (1 a and 3–4 a) and tended to become similar to surrounding undisturbed vegetation (no mound) as succession progressed. In no mound plots, the composition of plant functional groups was stable and plant diversity was high. Therefore, the later stage of succession in alpine meadows after disturbance had higher species richness and plant diversity (Zhang et al., 2009; Niu et al., 2019).

In this study, rodent disturbance significantly reduced species richness, coverage, and Simpson diversity index ($P < 0.05$; Table 1), but did not affect Shannon–Wiener diversity index and Pielou evenness index ($P > 0.05$; Table 1). However, plant community height increased significantly ($P < 0.05$; Table 1). Zokor-made mound disturbance led to partial changes in plant community structure without causing obvious damage to the overall structure. The niche breadth of perennial grasses increased after disturbance (e.g., *E. nutans* and *P. pratensis*), and the response of plant community structure tended to increase the proportion of fine forages as succession progressed. Zokor-made mound disturbance caused changes in soil nutrients and competitive relationships between monocotyledonous and dicotyledonous plant communities, which promoted an increase in grasses (Zhang et al., 2004). The fibrous root structure of monocotyledons enables efficient nutrient absorption and utilization, making them more competitive on disturbed soil (Adler et al., 2007). Species differ in their ecological response to disturbance (Zhang and Liu, 2003; Wang et al., 2008; Niu et al., 2020), with perennial forbs usually responding aggressively (Zhang et al., 2003). In this study, *K. capillifolia* (sedge) and *G. leucomelaena* (forb) showed stronger ecological responses in undisturbed sites, consistent with the dominance of *Kobresia* meadows in the region (Wang et al., 2006; Li et al., 2011; Hu et al., 2017). This was similar to Niu et al. (2020), who reported that dominant species in the community were fine forages and the proportion of sedges

increased significantly at the end of succession.

Analysis of competitive coexistence among species indicated that as succession progressed, the species that remained developmental included *K. macrantha* (perennial grass), *S. nigrescens*, and *R. tanguticus* (perennial forbs; Fig. 6 [Figure 6: see original paper]). These three species are the most common dominant species in alpine meadow communities of the QTP (Li et al., 2011; Mu et al., 2015; Shi et al., 2015; Hu et al., 2017). In the present study, the niche breadth of these species was also higher than that of other species (Fig. 2). With succession progress, species that transformed from declining to developmental were perennial grass *F. rubra*, perennial sedge *K. capillifolia*, perennial legume *T. himalaica*, and perennial forbs *P. nivea* and *G. ornata* (Fig. 6). The niche breadths of these species increased gradually with succession (Fig. 2). Similar to our results, *K. capillifolia* and *P. nivea* were also reported to be common dominant plant species with fine grazing capacity in alpine meadows of the QTP (Zhong et al., 2014; Guo et al., 2015; Xu et al., 2018; Wang et al., 2019). The forbs *D. caeruleum* and *G. paludosa* always remained declining with succession progress (Fig. 6), and their niche breadths were also smaller (Fig. 2). Additionally, perennial grasses *E. nutans* and *P. pratensis*, perennial forbs *T. farreri*, *V. eriogyne*, and *G. pylzowianum*, and annual forbs *H. elliptica* and *P. depressa* transformed from developmental to declining as succession progressed (Fig. 6), and niche breadths of these species decreased gradually over time (Fig. 2). This could be due to interspecific competition interactions, which play a vital role in determining community structure of either developmental or declining species, as interspecific competition became more obvious and niche overlap increased with succession progress (Cutler, 2010; Wang et al., 2012; Yang et al., 2018). As interspecific competition became more intense, niches tended to become more specialized and niche breadths decreased. Throughout the succession process, most annual plant species were in declining phase (e.g., *A. fatua*, *A. annua*, *G. paludosa*, *H. elliptica*, *G. leucomelaena*, *G. abaensis*, *P. kansuensis*, and *P. depressa*; Fig. 6). Annual species have poor competitive ability and generally cannot compete against more vigorous perennial species that have stronger competitive advantages (Yang et al., 2018). Perennial monocotyledons, which have fibrous root systems and strong ability to utilize soil nutrients, have particular advantages in heterogeneous environments following disturbance (Zhang et al., 2004; Adler et al., 2007).

Fig. 6 Coefficients of niche overlap of plant species under different types of zokor-made mound. (a) 1 a mound; (b) 3–4 a mound; (c) no mound. Bars are standard errors. * indicates significant difference among plant species at $P < 0.05$ level. S1–S41 indicate plant species.

5 Conclusions

This study showed that niche breadth of different plant species diverged after disturbance by zokor-made mounds. Mound construction did not cause obvious damage to the overall structure and function of plant communities in

alpine meadows, but led to partial changes in plant community structure that were conducive to stimulating regeneration and vitality of plant communities. Mounds increased the importance value and niche breadth of some perennial monocotyledonous forage species, which have greater competitive advantages in heterogeneous environments after disturbance. These perennial monocotyledons had obvious advantages in utilizing heterogeneous habitat resources and were often the main dominant species of alpine meadows. These dominant species with more extensive niche breadth had appropriate niche overlap with other species, ensuring their long-term ecological coexistence and adaptation. The composition of alpine meadow plant communities would succeed in the direction of increasing proportion of fine forages, with the result that disturbance may have improved the grazing capacity of alpine meadows.

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Appendix

[Appendix content with supplementary tables]

Note: Figure translations are in progress. See original paper for figures.