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

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**Abstract:** Mounds constructed by plateau zokors, which is widely distributed in alpine meadows significantly modified plant community structure. However, the variations of plant community structure under the disturbance of plateau zokor-made mound are less concerned. Therefore, we investigated the responses of plant community on zokor-made mound of different years (1 a and 3–4 a), and compared 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 mound, but plant heights were significantly increased, particularly in grasses and sedges. Several perennial forage species showed an increased importance value and niche breadth, including *Koeleria macrantha*, *Elymus nutans* and *Poa pratensis*. The effect of zokor-made mound on niche overlap showed that more intense interspecific competition produced a greater utilization of environmental resources. And this interspecific niche overlap was strengthened as succession progressed. The bare mound created by zokor burrowing activities provided a colonizing opportunity for non-dominant forage species, resulting in abundant plant species and plant diversity during the succession period. We concluded that presence of zokor-made mound was conducive to regeneration and vitality of plant community in alpine meadows, thus improving their resilience to anthropogenic stress.

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

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## 1 Introduction

The Qinghai-Tibetan Plateau (QTP), China is the world's largest alpine pastoral ecosystem. It provides ecological benefits of carbon sequestration, soil and water resource protection, aesthetic recreation and tourism, and economic benefits of 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) and a changing climate that is thawing permafrost and facilitating

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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 via 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 the alpine meadow of the QTP, China (Wang et al., 2008; Hu et al., 2017). This species is often described as a major pest due to its foraging, digging and mound-making activities producing highly visible changes to the meadow landscape. Its impact on plant diversity, biomass, soil organic carbon, temperature and soil water holding capacity is 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 the zokor-made mound than in the surrounding undisturbed soil (Li et al., 2009). Nevertheless, recent studies have suggested the positive ecological benefits of the plateau zokor, including increased soil water availability, soil organic carbon, and diverse plant communities across the meadow (Wang et al., 2008; Wu et al., 2017). Seed germination and seedling survival are both higher on the zokor-made mound (Bao et al., 2016; Hu et al., 2017). Moderate habitat disturbance by plateau zokor may stimulate species recruitment and increase meadow plant diversity, and therefore improve regeneration after a meadow has been overgrazed (Wu et al., 2015; Hu et al., 2017).

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

## 2 Materials and methods

### 2.1 Study area

The research area was located at the Hongyuan County Alpine Meadow Ecosystem Research Station of the 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. Average altitude is 3500 m a.s.l., annual mean temperature is 1.1°C and mean annual duration of snow cover is 76 d (Li et al., 2011).

### 2.2 Sampling and measurements

Plant coverage, height and frequency were recorded for each plant species in nine replicate plots of three mound treatments in September 2011. Treatments included the control of undisturbed meadow (no mound), and zokor-made mound aged one year (1 a) and three to four years (3–4 a) since construction, with plots selected randomly from the meadow. Mound had been abandoned by zokors at the time of study. The 1 a mound was constructed in August 2010, and at 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 time of study had a surface area of 0.4 $m^2$ and a height of 30–50 mm. Control plot of 1.0 $m^2$ was selected on site that showed 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 by the following equation:

$$\mathrm{IV}=(C_r+H_r+F_r)/3, \tag{1}$$

where $C_r$, $H_r$ and $F_r$ are the 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 formula of calculation of each index is given below:

$$H = -\sum_{i=1}^{S} P_i \ln P_i , \tag{2}$$

$$D = 1-\sum_{i=1}^{S} P_i^2 , \tag{3}$$

$$E=H/\ln S, \tag{4}$$

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

Six indices were used to assess the niche characteristics of plant community: (1) Levins niche breadth index ($\mathrm{NB_L}$; Hurlbert, 1978); (2) Shannon–Wiener niche breadth index ($\mathrm{NB_{SW}}$; Colwell and Futuyma, 1971); (3) Hurlbert niche breadth index ($\mathrm{NB_H}$; Hurlbert, 1978); (4) Levins coefficient of niche overlap ($O_{ik}$; Hurlbert, 1978); (5) ecological attributes ($\Delta O_{ik}$) and (6) ecological response rate ($R$; Zhang, 2018). The equations of each index are given below:

$$\mathrm{NB_L} = 1 / (n\sum_{j=1}^{r} P_{ij}^2) , \tag{5}$$

$$\mathrm{NB_{SW}} = -\sum_{j=1}^{r} P_{ij} \ln P_{ij} , \tag{6}$$

$$\mathrm{NB_H}=(n\mathrm{NB_L}-1)/(n-1), \tag{7}$$

$$O_{ik} = (\sum_{j=1}^{r} P_{ij}P_{kj}) / (\sum_{j=1}^{r} P_{ij}^2) , \tag{8}$$

$$\Delta O_{ik} = (\sum_{k=1}^{r} O_{ki} - \sum_{i=1}^{r} O_{ik}) , \tag{9}$$

$$R=\mathrm{NB}/\Delta O_{ik} \quad (i=k), \tag{10}$$

where $P_{ij}=n_{ij}/N_i$; $N_i = \sum_{j=1}^{r} n_{ij}$ ; $n_{ij}$ is the dominance of the $i^{\text{th}}$ population in the $j^{\text{th}}$ resource state; $P_{ij}$ is the proportion of the dominance of the $i^{\text{th}}$ population in the $j^{\text{th}}$ resource state to the total dominance of the $i^{\text{th}}$ population in all resource states; $n$ is the number of resources states; $P_{kj}$ is the proportion of the dominance of the $k^{\text{th}}$ population in the $j^{\text{th}}$ resource state to the total dominance of the $\mathrm{k}^{\text{th}}$ population in all resource states; $O_{ik}$ is the amount of occupied resources of population $k$ by population $i$; $O_{ki}$ is the amount of occupied resources of population $i$ by population $k$. If $O_{ik}>O_{ki}$, the population $i$ is developmental, otherwise, the population $k$ is declining; and NB is the niche breadth of plant species. The total niche overlap value is equal to the niche overlap value of all species pairs divided by the total number of species pairs in plant community.

All data were checked for normality and homogeneity of variance. Normality was tested by the Kolmogorov-Smirnov Z method ($P<0.05$) using a nonparametric test. Homogeneity of variance was tested by the Levene lest method ($P<0.05$). One-way analysis of variance (ANOVA) with Bonferroni's multiple range test ($P<0.05$) was performed to assess the effect of different types of zokor-made mound (1 a, 3–4 a and no mound) on plant species richness, height, $H$, $E$ and plant functional groups, which met the normality and homogeneity of variance. Data that failed the normality and homogeneity assumptions for parametric testing were analyzed by the nonparametric Kruskal-Wallis H test ($P<0.05$). $O_{ik}$ and $O_{ki}$ of plant species in the community were compared by 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 ($\mathrm{NB_{SW}}$, $\mathrm{NB_L}$ and $\mathrm{NB_H}$) and ecological response rate ($R$-$\mathrm{NB_{SW}}$, $R$-$\mathrm{NB_L}$ and $R$-$\mathrm{NB_H}$) of plant species were analyzed by the principal component analysis (PCA) in CANOCO 5.0 software (Version 5.0 for Windows; TerBraak and Smilauer, 2012) to identify the changes in niche characteristics among plant communities.

# 3 Results

## 3.1 Characteristics of plant community structure

Zokor-made mound had a reduced plant species richness, coverage and Simpson diversity index, but the Shannon–Wiener diversity and Pielou evenness indices were unaffected. Plant height in zokor-made mound 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). Grass coverage was greater in 3–4 a than both 1 a and no mound treatments, the latter of which was not significantly different. There was no significant difference in sedge coverage, but legume coverage of 1 a mound was significantly lower. Forb coverage was the highest in 1 a mound and the lowest in 3–4 a mound. Grass heights of both 1 a and 3–4 a mounds were significantly greater than that of no mound. Sedge height of 3–4 a mound was greater than those of 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 | |
|---|---|---|---|---|---|
| | 1 a | 3–4 a | No mound | *F* or *H* | *P* |
| Species richness | 18.44±4.50$^{ab}$ | 13.56±6.86$^{a}$ | 21.56±6.93$^{b}$ | $F_{2,24}$=3.81 | 0.037 |
| Coverage (%) | 82.56±3.17$^{a}$ | 91.56±4.82$^{b}$ | 97.44±1.33$^{b}$ | $H$=20.25 | <0.001 |
| Height (cm) | 13.48±0.72$^{a}$ | 13.50±1.08$^{a}$ | 12.43±0.69$^{b}$ | $F_{2,24}$=4.70 | 0.019 |
| Simpson diversity index | 0.958±0.005$^{a}$ | 0.941±0.013$^{a}$ | 0.967±0.001$^{b}$ | $H$=21.08 | <0.001 |
| Shannon–Wiener diversity index | 2.355±0.428 | 1.906±0.623 | 2.538±0.518 | $F_{2,24}$=3.40 | 0.050 |
| Pielou evenness index | 0.810±0.080 | 0.756±0.077 | 0.831±0.084 | $F_{2,24}$=2.05 | 0.151 |

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

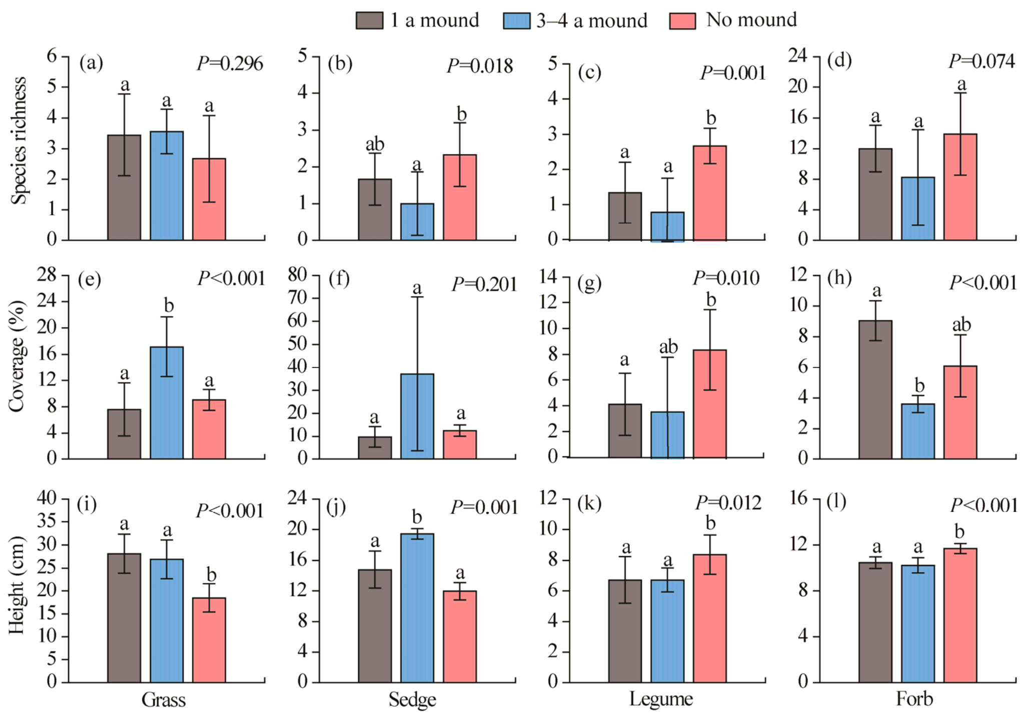


**Fig. 1** Species richness (a–d), coverage (e–h) and height (i–l) for each plant functional group and zokor-made mound type. Different lowercase letters indicate significant differences among different types of zokor-made mound at $P$<0.05 level.

## 3.2 Niche breadth of plant species

Zokor-made mound significantly affected the niche breadth of the 41 observed plant species (Table 2). The three formulae ($NB_{SW}$, $NB_L$ and $NB_H$) produced different values but similar trends across species (Fig. 2). Dominant species among treatments differed. Mound of 1 a was dominated by grasses (*Koeleria macrantha*, *Elymus nutans* and *Poa pratensis*) and forbs (*Stellaria infracta*, *Ranunculus tanguticus*, *Artemisia annua* and *Potentilla anserina)*. Mound of 3–4 a was also dominated by grasses (*P. pratensis*, *E. nutans* and *K. macrantha*) and forbs (*S. infracta* and *Lancea tibetica*). However, in no mound treatment, 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 ($\Delta O_{ik}$) for each plant species under different types of zokor-made mound

| No. | Species | Functional group | Life cycle | 1 a | | 3–4 a | | No mound | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | IV | $\Delta O_{ik}$ | IV | $\Delta O_{ik}$ | IV | $\Delta O_{ik}$ |
| S1 | *Koeleria macrantha* (Ledeb.) Schult. | Grass | P | 0.067 | 11.909 | 0.090 | 7.422 | 0.029 | 6.962 |
| S2 | *Elymus nutans* Griseb. | Grass | P | 0.048 | 9.767 | 0.076 | 12.948 | 0.014 | –10.019 |
| S3 | *Avena fatua* L. | Grass | A | 0.007 | –10.809 | - | - | - | - |
| S4 | *Poa pratensis* L. | Grass | P | 0.043 | 6.442 | 0.073 | 15.020 | 0.013 | –10.020 |
| S5 | *Festuca rubra* L. | Grass | P | 0.016 | –0.683 | 0.010 | –8.317 | 0.051 | 8.599 |
| S6 | *Festuca ovina* L. | Grass | P | - | - | 0.038 | –1.328 | 0.011 | –10.134 |
| S7 | *Kobresia capillifolia* (Decne.) C. B. Clarke | Sedge | P | 0.011 | –7.626 | - | - | 0.044 | 2.442 |
| S8 | *Trichophorum distigmaticum* (Kük.) T. V. Egorova | Sedge | P | 0.030 | 0.733 | 0.054 | –4.205 | 0.031 | 0.686 |
| S9 | *Carex kansuensis* Nelmes | Sedge | P | 0.026 | 1.543 | 0.087 | –0.848 | 0.037 | 7.012 |
| S10 | *Astragalus craibianus* G. Simpson | Legume | P | 0.025 | 6.854 | 0.012 | –4.787 | 0.025 | 4.189 |
| S11 | *Tibetia himalaica* (Baker) H. P. Tsui | Legume | P | 0.015 | –2.189 | 0.013 | 0.836 | 0.045 | 9.453 |
| S12 | *Oxytropis ochrocephala* Bunge | Legume | P | - | - | - | - | 0.033 | 9.053 |
| S13 | *Artemisia annua* L. | Forb | A | 0.104 | 7.983 | 0.008 | –4.603 | - | - |
| S14 | *Anaphalis lactea* Maxim. | Forb | P | 0.047 | 5.788 | 0.004 | –8.326 | 0.045 | 8.129 |
| S15 | *Saussurea nigrescens* Maxim. | Forb | P | 0.026 | 6.589 | 0.014 | 1.703 | 0.062 | 10.708 |
| S16 | *Taraxacum lugubre* Dahlst. | Forb | P | 0.003 | –10.802 | - | - | 0.009 | –5.799 |
| S17 | *Cirsium periacanthaceum* C. Shih | Forb | P | 0.011 | –10.812 | - | - | - | - |
| S18 | *Leontopodium nanum* (Hook.f. & Thomson ex Hook.f. & Thomson) Hand.-Mazz. | Forb | P | - | - | 0.004 | –8.314 | - | - |
| S19 | *Leontopodium stracheyi* (Hook.f.) C. B. Clarke ex Hemsl. | Forb | P | - | - | - | - | 0.012 | –5.540 |
| S20 | *Ajania tenuifolia* Tzvelev | Forb | P | - | - | - | - | 0.014 | –0.940 |
| S21 | *Saussurea graminea* Dunn | Forb | P | - | - | - | - | 0.005 | –9.958 |
| S22 | *Potentilla anserina* L. | Forb | P | 0.033 | 7.290 | 0.011 | –8.363 | 0.029 | 9.214 |
| S23 | *Potentilla nivea* L. | Forb | P | 0.004 | –10.275 | 0.012 | 1.471 | 0.023 | 4.662 |
| S24 | *Delphinium caeruleum* Jacquem. ex Cambess. | Forb | P | 0.011 | –8.966 | 0.008 | –8.318 | 0.018 | –5.468 |
| S25 | *Trollius farreri* Stapf | Forb | P | 0.015 | 2.063 | 0.010 | 1.871 | 0.006 | –9.927 |
| S26 | *Ranunculus tanguticus* (Maxim.) Ovcz. | Forb | P | 0.037 | 8.548 | 0.012 | 1.821 | 0.033 | 10.286 |
| S27 | *Anemone rivularis* Buch.-Ham. ex DC. | Forb | P | 0.019 | 1.721 | 0.005 | –8.314 | 0.035 | 11.582 |

To be continued

Continued

| No. | Species | Functional group | Life cycle | 1 a | | 3–4 a | | No mound | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | IV | $\Delta O_{ik}$ | IV | $\Delta O_{ik}$ | IV | $\Delta O_{ik}$ |
| S28 | *Gentianopsis paludosa* (Hook. f.) Ma | Forb | A | 0.007 | –10.278 | 0.008 | –4.527 | 0.007 | –9.923 |
| S29 | *Halenia elliptica* D. Don | Forb | A | 0.029 | 6.296 | 0.005 | –8.319 | 0.017 | –1.326 |
| S30 | *Gentiana ornata* (D.Don) Wall. ex Griseb. | Forb | P | 0.008 | –9.063 | 0.007 | –4.538 | 0.036 | 6.973 |
| S31 | *Gentiana leucomelaena* Maxim. | Forb | A | - | - | - | - | 0.014 | 2.500 |
| S32 | *Gentiana abaensis* T. N. Ho | Forb | A | - | - | - | - | 0.006 | –10.050 |
| S33 | *Lancea tibetica* Hook. f. & Thomson | Forb | P | 0.011 | –4.665 | 0.025 | 11.953 | 0.012 | –0.878 |
| S34 | *Veronica eriogyne* H. Winkl. | Forb | P | 0.031 | 5.965 | 0.012 | 1.923 | 0.017 | –5.860 |
| S35 | *Pedicularis kansuensis* Maxim. | Forb | A | - | - | 0.004 | –8.327 | 0.005 | –9.936 |
| S36 | *Epilobium royleanum* Hausskn. | Forb | P | 0.010 | –9.068 | - | - | - | - |
| S37 | *Plantago depressa* Willd. | Forb | A | 0.020 | 2.053 | 0.024 | 5.694 | 0.010 | –5.725 |
| S38 | *Stellaria infracta* Maxim. | Forb | P | 0.027 | 8.462 | 0.037 | 14.024 | - | - |
| S39 | *Equisetum arvense* L. | Forb | P | 0.006 | –7.658 | 0.006 | –4.123 | - | - |
| S40 | *Geranium pylzowianum* Maxim. | Forb | P | 0.022 | 2.887 | - | - | 0.009 | –5.624 |
| S41 | *Allium sikkimense* Baker | Forb | P | - | - | 0.030 | 5.650 | 0.026 | 4.678 |

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

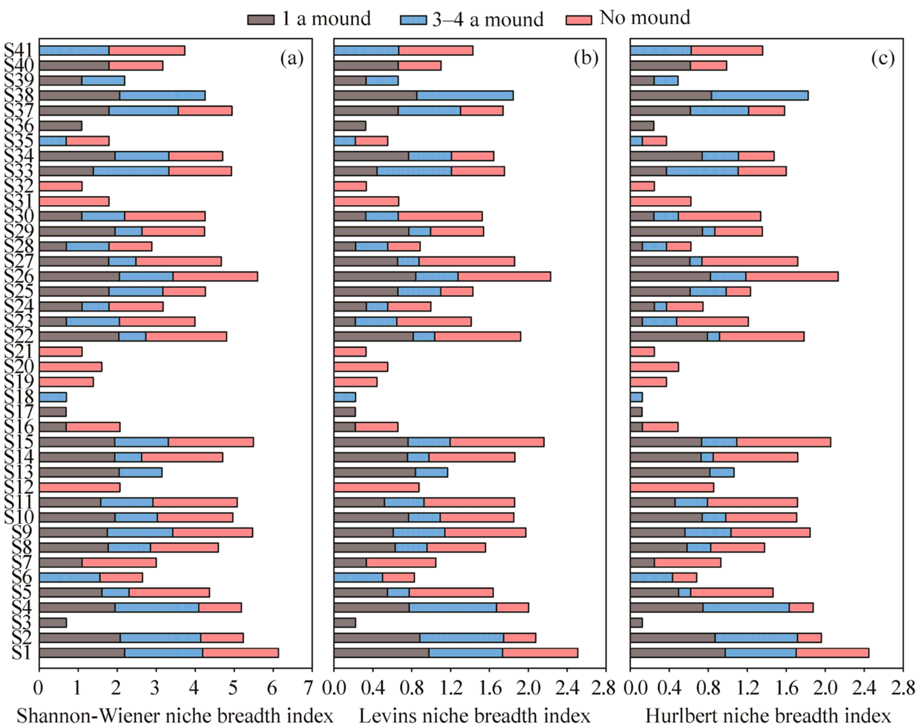


**Fig. 2** Shannon-Wiener niche breadth index (a), Levins niche breadth index (b) and Hurlbert niche breadth index (c) of plant species under different types of zokor-made mound. S1–S41 indicate plant species.

### 3.3 Niche overlap of plant species

Most species pairs had niche overlap in 1 a (91.18%; Table S1), and 3–4 a mounds (87.19%; Table S2), and 100.00% in no mound (Table S3). The proportions of species pairs with niche overlap of >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 mound, respecitively; 47.41%, 40.52%, 36.21%, 32.76% and 19.33% in 3–4 a mound, respectively; and 55.35%, 46.97%, 38.59%, 27.45% and 9.18% in no-mound, respectively. The total niche overlap in 1 a mound, 3–4 a mound and no mound was 58.32%, 59.31% and 65.91%, respectively. Niche overlap of plant species was initially small in new zokor-made mound and increased gradually as the succession progressed. The proportions of specie pairs in 3–4 a mound with niche overlap of >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 of 1 a mound and no mound, respectively. These results indicate that competition among plant species increases over time, thus resulting in the increase of the interspecies niche overlap.

### 3.4 Ecological response rate (*R*) of plant species

According to the $\Delta O_{ik}$, we found 18 developmental and 13 declining populations in 1 a mound (Table 2). The main developmental populations were *K. macrantha*, *E. nutans*, *R. tanguticus*, *S. infracta* and *A. annua* and the main declining populations were *C. periacanthaceum*, *A. fatua*, *T. lugubre*, *G. paludosa* and *P. nivea*. In 3–4 a mound, we found 13 developmental and 16 declining populations. The main developmental populations were *P. pratensis*, *S. infracta*, *E. nutans* and *L. tibetica* and 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, we found 17 developmental populations 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 and *F. ovina*, *G. abaensis*, *P. pratensis*, *E. nutans*, *S. graminea*, *P. kansuensis*, *T. farreri* and *G. paludosa* were the main declining populations.

The ecological response rates of different populations to the habitat are represented by the values of *R*. Among the developmental populations, *T. distigmaticum* ($R$-$NB_{SW}$=2.41, $R$-$NB_L$=0.86 and $R$-$NB_H$=0.80), *C. kansuensis* ($R$-$NB_{SW}$=1.13, $R$-$NB_L$=0.40 and $R$-$NB_H$=0.36) and *A. rivularis* ($R$-$NB_{SW}$=1.04, $R$-$NB_L$=0.38 and $R$-$NB_H$=0.35) showed the higher *R* values, whereas, *F. rubra* ($R$-$NB_{SW}$= –2.35, $R$-$NB_L$= –0.81 and $R$-$NB_H$= –0.73) was the most declining population with a larger *R* in 1 a mound (Fig. 3). In 3–4 a mound, *T. himalaica* ($R$-$NB_{SW}$ =1.60, $R$-$NB_L$=0.49 and $R$-$NB_H$=0.40) was the main developmental population and *C. kansuensis* ($R$-$NB_{SW}$= –1.97, $R$-$NB_L$= –0.63 and $R$-$NB_H$= –0.56) and *F. ovina* ($R$-$NB_{SW}$= –1.17, $R$-$NB_L$= –0.38 and $R$-$NB_H$= –0.33) (Fig. 3) were the declining populations. In no mound, *T. distigmaticum* was the main developmental population ($R$-$NB_{SW}$=2.54, $R$-$NB_L$=0.88 and $R$-$NB_H$=0.81), and *L. tibetica* ($R$-$NB_{SW}$= –1.82, $R$-$NB_L$= –0.62 and $R$-$NB_H$= –0.56), *A. tenuifolia* ($R$-$NB_{SW}$ = –1.71, $R$-$NB_L$= –0.59 and $R$-$NB_H$ = –0.53) and *H. elliptica* ($R$-$NB_{SW}$= –1.21, $R$-$NB_L$= –0.41 and $R$-$NB_H$= –0.37) were the main declining populations (Fig. 3).

### 3.5 Responses of niche breadth and *R* to zokor-made mound

PCA ordination of niche breadth and *R* of plant species showed that the cumulative contribution rates of variance of the two principal components were 86.67% and 89.02%, respectively (Figs. 4 and 5). Three types of mound were clearly separated by niche characteristics. *Elymus nutans*, *P. pratensis*, *A. annua* and *S. infracta* occupied larger areas in new mound (Fig. 4). *E. nutans*, *P. pratensis*, *L. nanum*, *S. infracta* and *E. arvense* appeared the most sensitive species in 3–4 a mound, three of which (*E. nutans*, *P. pratensis* and *S. infracta*) had a larger niche breadth compared with other species. In no mound, *F. rubra*, *K. capillifolia*, *O. ochrocephala*, *A. tenuifolia*, *S. graminea*, *L. stracheyi*, *T. lugubre*, *A. rivularis*, *G. leucomelaena*, *G. abaensis* and *G. ornata* had a higher relevant 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 a larger niche breadth, which indicated that the composition of plant functional groups was stable and the plant diversity was high in no mound treatment (Fig. 4; Table 2).

PCA ordination of *R* in 1 a mound 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). *R* values of *A. rivularis*, *G. pylzowianum*, *P. depressa* and *T. farreri* were higher. In 3–4 a mound, *S. nigrescens*, *P. nivea*, *R. tanguticus* and *V. eriogyne* had higher *R* values, therefore they were the most sensitive species (Fig. 5). However, PCA ordination of *R* in no mound showed that *K. macrantha*, *F. rubra*, *K. capillifolia*, *O. ochrocephala*, *A. sikkimense*, *G. leucomelaena* and *G. ornate* had a higher correlation with habitat compared with other species (Fig. 5). Sedge *K. capillifolia* and forb *G. leucomelaena* showed higher *R* values.

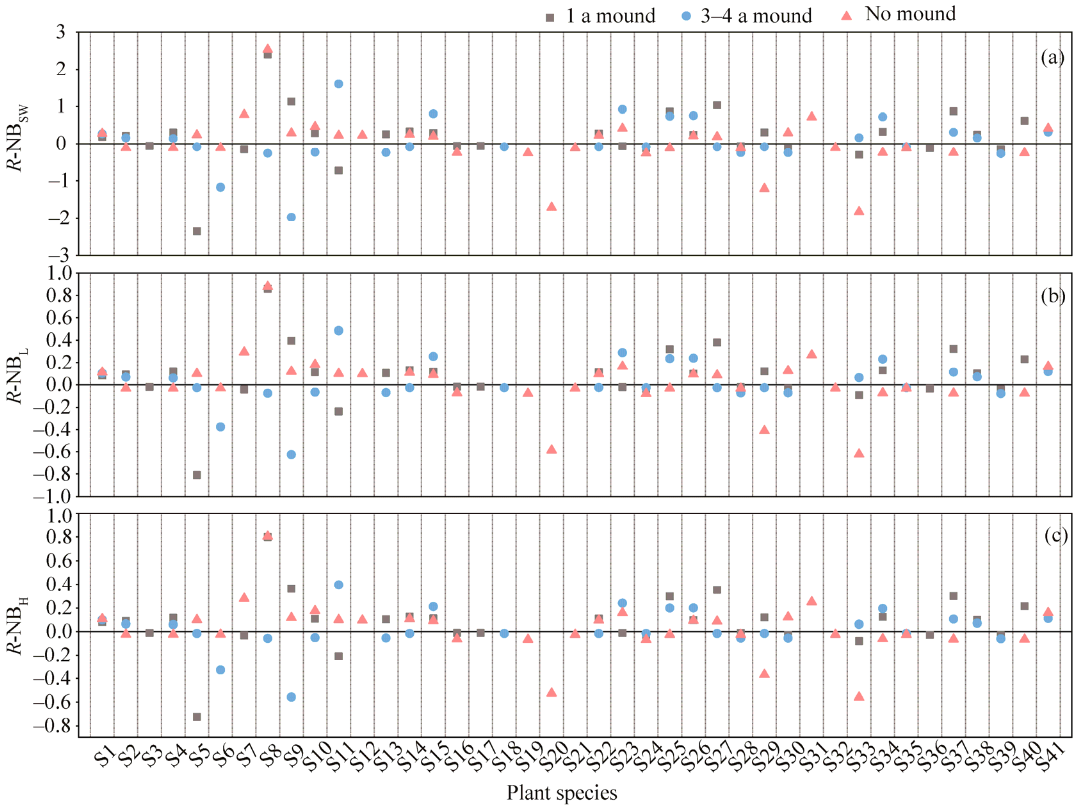


**Fig. 3** Ecological response rates ($R$) of plant species under different types of zokor-made mound. $R$-NB$_{SW}$, ecological response rate of Shannon–Wiener index (a); $R$-NB$_{L}$, ecological response rate of Levins index (b); $R$-NB$_{H}$, ecological response rate of Hurlbert index (c). S1–S41 indicate plant species.

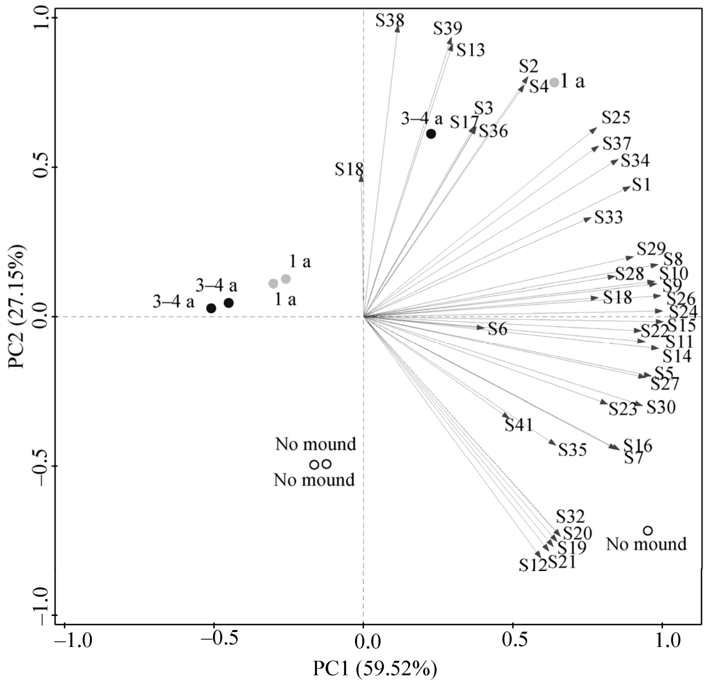


**Fig. 4** Principal components analysis (PCA) of niche breadth under different types of zokor-made mound. S1–S41 indicate plant species.

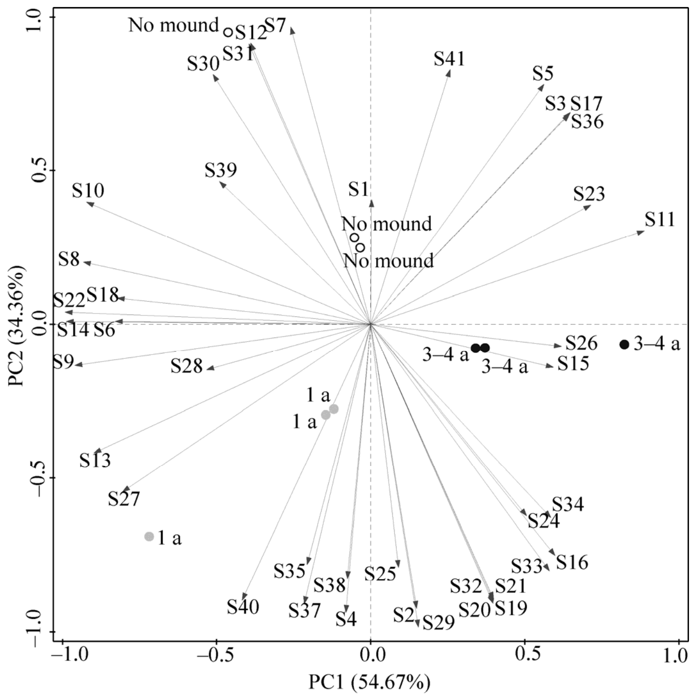


**Fig. 5** Principal components analysis (PCA) of ecological response rate under different types of zokor-made mound. S1–S41 indicate plant species.

## 4 Discussion

Disturbance by burrowing rodents is widespread across ecosystems. In tundra grasslands, rodents had positive effects on nutrient cycling by modifying the 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 the 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, as selectively foraging on two legumes and one coneflower, voles altered plant community structure and reduced plant diversity (Howe and Brown, 1999). In grasslands, disturbance by rodents reduced productivity (Maron et al., 2014). Based on this study, we believed that disturbance by rodents also had a positive or negative effect on the plant community in alpine meadow. Plateau zokor, a typical alpine meadow rodent, plays an important role in ecosystem function, such as soil nutrient cycling, soil structure, vegetation composition and so on, creating heterogeneous habitat patches and being regarded as ecosystem engineers (Zhang and Liu, 2003). The mound-making by plateau zokor is an important determinant of plant community composition in the alpine meadow (Hu et al., 2017), however, how the zokor-made mound disturbance affected niche characteristics of plant community in alpine meadow had been often ignored.

Niche breadth can be used as an indicator to measure the scale of species' utilization of environments or resources. Usually, the species with a higher importance value can use more resources or tolerate variable environmental conditions and distribute more widely, resulting in the larger niches (Dostál et al., 2016; Pannek et al., 2016). The larger the niche breadth of the 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, the heterogeneous habitat created by the original community after disturbance causes the release of niche space. Then, the species affect community structure by competing or pre-empting niche space in heterogeneous habitat (Yang et al., 2018). Generally, because each species has an equal competitive opportunity to colonize bare zokor-made mound to occupy the niche during succession process, different types of forages could coexist, thus resulting in more abundant plant species in the climax community. Our study was similar to the results of Yang et al. (2018) and Niu et al. (2020), in that the composition characteristics of plant community were different at earlier stages of succession (1 a and 3–4 a) and inclined to become similar to surrounding undisturbed vegetation (no mound) as succession progressed. In no mound, the composition of functional groups of plant community was stable and plant diversity was high. Therefore, the later stage of succession in the alpine meadow after disturbance had higher species richness and plant diversity (Zhang et al., 2009; Niu et al., 2019).

In this study, disturbance by rodents significantly reduced the 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, the height of plant community increased significantly ($P$<0.05; Table 1). The disturbance of zokor-made mound led to partial changes in the plant community structure, but there was no obvious damage to the overall structure of the plant community. 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. The disturbance caused by zokor-made mound led to changes of soil nutrients and the competitive relationship between monocotyledons and dicotyledons plant communities, which promoted an increase of grasses (Zhang et al., 2004). The fibrous root structure of monocotyledons enables efficient nutrient absorption and utilization, thus 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 a stronger ecological response in undisturbed sites, which is consistent with the dominance of *Kobresia* meadow in the region (Wang et al., 2006; Li et al., 2011; Hu et al., 2017). It was similar to the result of Niu et al. (2020), in that the dominant species in the community were fine forages, and the proportion of sedges significantly increased at the end of succession.

Analysis of competitive coexistence among species indicated that as succession progresses, the species that remained developmental included *K. macrantha* (perennial grass), *S. nigrescens* and *R. tanguticus* (perennial forbs; Fig. 6). These three species are the most common dominant species in alpine meadow communities of 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 those of other species (Fig. 2). With the progress of succession, the species that transformed from declining to developmental were perennial grass *F. rubra*, perennial sedge *K. capillifolia*, perennial legume *T. himalaica* and perennial forb *P. nivea* and *G. ornata* (Fig. 6). The niche breadths of these species increased gradually with the succession (Fig. 2). Similar to our results, *K. capillifolia* and *P. nivea* were also reported to be the common dominant plant species with fine grazing capacity in the alpine meadow of QTP (Zhong et al., 2014; Guo et al., 2015; Xu et al., 2018; Wang et al., 2019). The forb *D. caeruleum* and *G. paludosa* always remained declining with the progress of succession (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 the interspecific competition interaction, which plays a vital role in determining community structure of either developmental or declining species, the interspecific competition became more obvious and the niche overlap increased as succession progressed (Cutler, 2010; Wang et al., 2012; Yang et al., 2018). Interspecific competition became more intense, their niches tended to be more specialized and their niche breadths decreased. In the whole process of succession, most of 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 they are unable to compete against the more vigorous perennial species that have a stronger advantage in competition (Yang et al., 2018). Perennial monocotyledons, which have fibrous root system and strong ability to utilize soil nutrients, in particular have advantages in the heterogeneous environment following disturbance (Zhang et al., 2004; Adler et al., 2007).

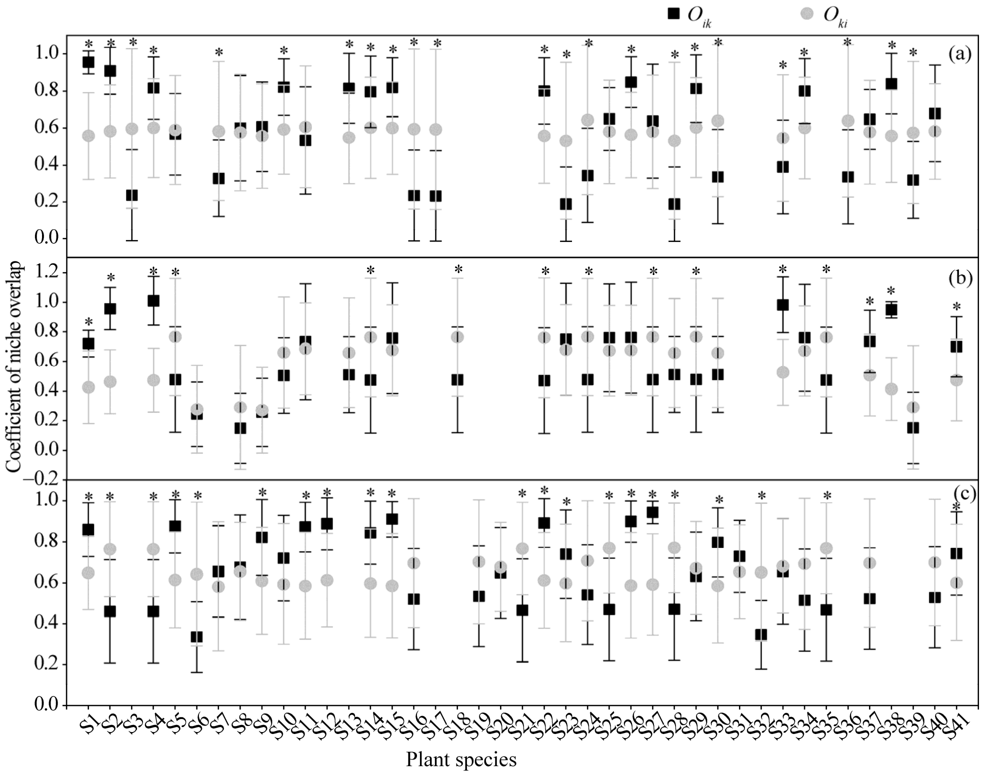


**Fig. 6** Coefficients of niche overlap of plant species under different types of zokor-made mound. (a), 1 a mound; (b), 3–4 a mound; (c), no mound. Bars are standard errors. * indicates significant difference among plant species at $P<0.05$ level. S1–S41 indicate plant species.

## 5 Conclusions

This study showed that niche breadth of different plant species diverged after disturbance by zokor-made mound. Mound construction didn't cause obvious damage to the overall structure and function of plant community in alpine meadow, but led to partial changes in plant community structure, which was conducive to stimulate the regeneration and vitality of plant community in alpine meadow. Mound increased the importance value and niche breadth of some perennial monocotyledonous forage species, which have more competitive advantages in the heterogeneous environment after disturbance. These perennial monocotyledonous species had obvious advantages in the utilization of heterogeneous habitat resources, and these perennial monocotyledons were often the main dominant species of alpine meadow. 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 community would succeed in the direction of increasing proportion of fine forages, with the result that disturbance may have improved the grazing capacity of alpine meadow.

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# Appendix

**Table S1** Coefficient of niche overlap in 1 a zokor-made mound

| No. | S1 | S2 | S3 | S4 | S5 | S7 | S8 | S9 | S10 | S11 | S13 | S14 | S15 | S16 | S17 | S22 | S23 | S24 | S25 | S26 | S27 | S28 | S29 | S30 | S33 | S34 | S36 | S37 | S38 | S39 | S40 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S1 | | 0.86 | 0.18 | 0.75 | 0.52 | 0.35 | 0.65 | 0.60 | 0.71 | 0.52 | 0.82 | 0.74 | 0.72 | 0.18 | 0.18 | 0.82 | 0.21 | 0.34 | 0.69 | 0.83 | 0.67 | 0.21 | 0.75 | 0.33 | 0.45 | 0.76 | 0.33 | 0.69 | 0.85 | 0.35 | 0.66 |
| S2 | 0.95 | | 0.24 | 0.88 | 0.63 | 0.23 | 0.73 | 0.49 | 0.84 | 0.58 | 0.83 | 0.86 | 0.84 | 0.24 | 0.24 | 0.72 | 0.24 | 0.38 | 0.60 | 0.79 | 0.75 | 0.24 | 0.88 | 0.37 | 0.51 | 0.88 | 0.37 | 0.61 | 0.77 | 0.21 | 0.59 |
| S3 | 0.81 | 0.95 | | 1.06 | 1.09 | 0.48 | 0.00 | 0.94 | 1.03 | 0.00 | 0.97 | 0.91 | 0.92 | 1.00 | 0.99 | 0.87 | 0.00 | 0.00 | 0.51 | 0.73 | 0.00 | 0.00 | 0.97 | 0.00 | 0.00 | 0.86 | 0.00 | 0.48 | 0.92 | 0.46 | 0.95 |
| S4 | 0.95 | 1.01 | 0.30 | | 0.73 | 0.27 | 0.71 | 0.50 | 0.82 | 0.54 | 0.77 | 0.97 | 0.84 | 0.30 | 0.30 | 0.72 | 0.13 | 0.40 | 0.66 | 0.72 | 0.69 | 0.13 | 0.99 | 0.40 | 0.42 | 0.98 | 0.40 | 0.67 | 0.76 | 0.25 | 0.68 |
| S5 | 0.92 | 1.01 | 0.44 | 1.02 | | 0.21 | 0.60 | 0.52 | 0.80 | 0.31 | 0.95 | 0.90 | 0.75 | 0.44 | 0.44 | 0.79 | 0.17 | 0.18 | 0.73 | 0.67 | 0.51 | 0.17 | 0.95 | 0.17 | 0.55 | 0.94 | 0.17 | 0.75 | 0.86 | 0.20 | 0.58 |
| S7 | 1.02 | 0.60 | 0.32 | 0.62 | 0.34 | | 0.24 | 1.15 | 0.58 | 0.29 | 0.75 | 0.59 | 0.59 | 0.31 | 0.29 | 1.23 | 0.00 | 0.30 | 1.08 | 0.94 | 0.30 | 0.00 | 0.62 | 0.27 | 0.00 | 0.57 | 0.27 | 1.02 | 1.17 | 0.99 | 1.02 |
| S8 | 1.01 | 1.03 | 0.00 | 0.87 | 0.52 | 0.13 | | 0.30 | 0.73 | 0.74 | 0.76 | 0.89 | 0.78 | 0.00 | 0.00 | 0.65 | 0.26 | 0.50 | 0.64 | 0.74 | 0.99 | 0.26 | 0.89 | 0.50 | 0.67 | 0.93 | 0.50 | 0.67 | 0.70 | 0.12 | 0.48 |
| S9 | 0.96 | 0.71 | 0.34 | 0.63 | 0.47 | 0.62 | 0.31 | | 0.74 | 0.32 | 0.91 | 0.58 | 0.68 | 0.34 | 0.34 | 1.06 | 0.21 | 0.18 | 0.77 | 0.97 | 0.37 | 0.21 | 0.61 | 0.16 | 0.21 | 0.57 | 0.16 | 0.74 | 1.07 | 0.62 | 0.80 |
| S10 | 0.91 | 0.97 | 0.30 | 0.82 | 0.58 | 0.25 | 0.60 | 0.59 | | 0.65 | 0.85 | 0.81 | 0.97 | 0.30 | 0.30 | 0.72 | 0.32 | 0.38 | 0.50 | 0.94 | 0.70 | 0.32 | 0.83 | 0.38 | 0.43 | 0.80 | 0.38 | 0.50 | 0.78 | 0.24 | 0.65 |
| S11 | 0.97 | 0.99 | 0.00 | 0.81 | 0.33 | 0.19 | 0.90 | 0.38 | 0.95 | | 0.65 | 0.90 | 1.04 | 0.00 | 0.00 | 0.60 | 0.30 | 0.71 | 0.50 | 0.95 | 1.03 | 0.30 | 0.88 | 0.71 | 0.49 | 0.89 | 0.71 | 0.51 | 0.64 | 0.17 | 0.68 |
| S13 | 0.95 | 0.88 | 0.26 | 0.71 | 0.62 | 0.30 | 0.57 | 0.66 | 0.77 | 0.40 | | 0.64 | 0.70 | 0.26 | 0.26 | 0.89 | 0.32 | 0.18 | 0.65 | 0.86 | 0.58 | 0.32 | 0.67 | 0.17 | 0.56 | 0.67 | 0.16 | 0.66 | 0.94 | 0.30 | 0.54 |
| S14 | 0.96 | 1.01 | 0.27 | 0.99 | 0.66 | 0.26 | 0.74 | 0.47 | 0.82 | 0.62 | 0.71 | | 0.88 | 0.27 | 0.27 | 0.68 | 0.12 | 0.48 | 0.62 | 0.73 | 0.74 | 0.12 | 1.01 | 0.48 | 0.38 | 1.00 | 0.48 | 0.63 | 0.71 | 0.24 | 0.72 |
| S15 | 0.92 | 0.98 | 0.27 | 0.86 | 0.54 | 0.26 | 0.65 | 0.55 | 0.98 | 0.71 | 0.77 | 0.88 | | 0.27 | 0.27 | 0.69 | 0.25 | 0.48 | 0.51 | 0.91 | 0.74 | 0.25 | 0.88 | 0.48 | 0.39 | 0.86 | 0.48 | 0.50 | 0.74 | 0.24 | 0.72 |
| S16 | 0.80 | 0.95 | 1.00 | 1.06 | 1.09 | 0.46 | 0.00 | 0.93 | 1.03 | 0.00 | 0.97 | 0.91 | 0.93 | | 1.00 | 0.86 | 0.00 | 0.00 | 0.49 | 0.73 | 0.00 | 0.00 | 0.98 | 0.00 | 0.00 | 0.86 | 0.00 | 0.46 | 0.91 | 0.45 | 0.95 |
| S17 | 0.80 | 0.95 | 1.00 | 1.06 | 1.09 | 0.44 | 0.00 | 0.93 | 1.03 | 0.00 | 0.98 | 0.91 | 0.93 | 1.00 | | 0.86 | 0.00 | 0.00 | 0.47 | 0.73 | 0.00 | 0.00 | 0.98 | 0.00 | 0.00 | 0.86 | 0.00 | 0.45 | 0.91 | 0.43 | 0.95 |
| S22 | 0.99 | 0.78 | 0.24 | 0.68 | 0.53 | 0.50 | 0.50 | 0.80 | 0.68 | 0.38 | 0.91 | 0.63 | 0.64 | 0.23 | 0.23 | | 0.20 | 0.24 | 0.81 | 0.87 | 0.51 | 0.20 | 0.66 | 0.22 | 0.40 | 0.65 | 0.22 | 0.80 | 1.02 | 0.50 | 0.70 |
| S23 | 0.91 | 0.96 | 0.00 | 0.47 | 0.43 | 0.00 | 0.75 | 0.59 | 1.12 | 0.69 | 1.21 | 0.39 | 0.87 | 0.00 | 0.00 | 0.74 | | 0.00 | 0.42 | 1.25 | 0.90 | 1.00 | 0.42 | 0.00 | 1.00 | 0.46 | 0.00 | 0.44 | 0.89 | 0.00 | 0.00 |
| S24 | 0.99 | 1.00 | 0.00 | 0.94 | 0.30 | 0.30 | 0.95 | 0.33 | 0.88 | 1.11 | 0.44 | 1.10 | 1.10 | 0.00 | 0.00 | 0.59 | 0.00 | | 0.59 | 0.83 | 1.07 | 0.00 | 1.06 | 0.99 | 0.29 | 1.06 | 0.99 | 0.58 | 0.59 | 0.27 | 0.96 |
| S25 | 1.02 | 0.80 | 0.17 | 0.78 | 0.61 | 0.55 | 0.61 | 0.71 | 0.59 | 0.40 | 0.83 | 0.72 | 0.59 | 0.16 | 0.16 | 1.00 | 0.14 | 0.30 | | 0.79 | 0.57 | 0.14 | 0.75 | 0.28 | 0.45 | 0.76 | 0.28 | 1.00 | 1.01 | 0.54 | 0.69 |
| S26 | 0.97 | 0.82 | 0.19 | 0.66 | 0.44 | 0.37 | 0.55 | 0.70 | 0.85 | 0.59 | 0.85 | 0.66 | 0.82 | 0.19 | 0.19 | 0.84 | 0.33 | 0.33 | 0.62 | | 0.64 | 0.33 | 0.67 | 0.32 | 0.42 | 0.66 | 0.32 | 0.61 | 0.88 | 0.37 | 0.68 |
| S27 | 1.00 | 1.01 | 0.00 | 0.81 | 0.43 | 0.15 | 0.95 | 0.35 | 0.82 | 0.82 | 0.75 | 0.86 | 0.87 | 0.00 | 0.00 | 0.64 | 0.30 | 0.54 | 0.57 | 0.83 | | 0.30 | 0.85 | 0.54 | 0.62 | 0.88 | 0.54 | 0.59 | 0.69 | 0.14 | 0.52 |
| S28 | 0.91 | 0.96 | 0.00 | 0.47 | 0.43 | 0.00 | 0.75 | 0.59 | 1.12 | 0.69 | 1.20 | 0.40 | 0.87 | 0.00 | 0.00 | 0.74 | 1.00 | 0.00 | 0.42 | 1.25 | 0.90 | | 0.42 | 0.00 | 1.00 | 0.46 | 0.00 | 0.44 | 0.89 | 0.00 | 0.00 |
| S29 | 0.95 | 1.01 | 0.28 | 1.00 | 0.68 | 0.27 | 0.73 | 0.48 | 0.82 | 0.59 | 0.73 | 0.99 | 0.87 | 0.28 | 0.28 | 0.70 | 0.12 | 0.46 | 0.64 | 0.73 | 0.72 | 0.12 | | 0.45 | 0.40 | 0.99 | 0.45 | 0.65 | 0.74 | 0.25 | 0.71 |
| S30 | 1.00 | 1.00 | 0.00 | 0.94 | 0.29 | 0.28 | 0.96 | 0.30 | 0.88 | 1.12 | 0.42 | 1.11 | 1.11 | 0.00 | 0.00 | 0.56 | 0.00 | 1.00 | 0.56 | 0.83 | 1.08 | 0.00 | 1.07 | | 0.28 | 1.07 | 1.00 | 0.55 | 0.56 | 0.25 | 0.96 |
| S33 | 0.99 | 1.03 | 0.00 | 0.74 | 0.69 | 0.00 | 0.96 | 0.30 | 0.75 | 0.58 | 1.06 | 0.66 | 0.67 | 0.00 | 0.00 | 0.73 | 0.50 | 0.22 | 0.67 | 0.80 | 0.91 | 0.50 | 0.69 | 0.21 | | 0.75 | 0.21 | 0.72 | 0.84 | 0.00 | 0.20 |
| S34 | 0.96 | 1.01 | 0.25 | 0.99 | 0.68 | 0.25 | 0.77 | 0.45 | 0.80 | 0.60 | 0.73 | 0.99 | 0.85 | 0.25 | 0.25 | 0.69 | 0.13 | 0.46 | 0.65 | 0.72 | 0.75 | 0.13 | 1.00 | 0.46 | 0.43 | | 0.46 | 0.67 | 0.73 | 0.23 | 0.68 |
| S36 | 1.00 | 1.00 | 0.00 | 0.94 | 0.28 | 0.28 | 0.96 | 0.30 | 0.88 | 1.12 | 0.42 | 1.11 | 1.11 | 0.00 | 0.00 | 0.55 | 0.00 | 1.00 | 0.55 | 0.83 | 1.08 | 0.00 | 1.07 | 1.00 | 0.28 | 1.07 | | 0.54 | 0.55 | 0.25 | 0.97 |
| S37 | 1.02 | 0.81 | 0.16 | 0.79 | 0.63 | 0.52 | 0.64 | 0.68 | 0.58 | 0.40 | 0.84 | 0.72 | 0.58 | 0.15 | 0.15 | 0.99 | 0.15 | 0.29 | 1.00 | 0.78 | 0.58 | 0.15 | 0.76 | 0.27 | 0.48 | 0.77 | 0.27 | | 1.00 | 0.51 | 0.67 |
| S38 | 0.98 | 0.80 | 0.24 | 0.69 | 0.55 | 0.46 | 0.52 | 0.76 | 0.70 | 0.39 | 0.93 | 0.63 | 0.66 | 0.24 | 0.24 | 0.97 | 0.23 | 0.23 | 0.78 | 0.87 | 0.53 | 0.23 | 0.67 | 0.21 | 0.44 | 0.66 | 0.21 | 0.77 | | 0.46 | 0.66 |
| S39 | 1.03 | 0.57 | 0.31 | 0.59 | 0.34 | 1.00 | 0.22 | 1.16 | 0.56 | 0.27 | 0.75 | 0.56 | 0.56 | 0.30 | 0.29 | 1.24 | 0.00 | 0.28 | 1.09 | 0.95 | 0.28 | 0.00 | 0.59 | 0.25 | 0.00 | 0.54 | 0.25 | 1.03 | 1.18 | | 1.03 |
| S40 | 0.98 | 0.79 | 0.32 | 0.79 | 0.49 | 0.52 | 0.46 | 0.73 | 0.75 | 0.54 | 0.68 | 0.82 | 0.83 | 0.32 | 0.32 | 0.86 | 0.00 | 0.48 | 0.69 | 0.86 | 0.52 | 0.00 | 0.82 | 0.48 | 0.14 | 0.78 | 0.48 | 0.67 | 0.85 | 0.51 | |

Note: S1–S40 indicate plant species.

**Table S2** Coefficient of niche overlap in 3–4 a zokor-made mound

| No. | S1 | S2 | S4 | S5 | S6 | S8 | S9 | S10 | S11 | S13 | S14 | S15 | S18 | S22 | S23 | S24 | S25 | S26 | S27 | S28 | S29 | S30 | S33 | S34 | S35 | S37 | S38 | S39 | S41 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S1 | | 0.94 | 0.97 | 0.18 | 0.41 | 0.30 | 0.43 | 0.37 | 0.39 | 0.37 | 0.18 | 0.43 | 0.18 | 0.18 | 0.42 | 0.18 | 0.44 | 0.43 | 0.18 | 0.37 | 0.18 | 0.37 | 0.74 | 0.44 | 0.18 | 0.67 | 0.99 | 0.30 | 0.68 |
| S2 | 0.83 | | 0.90 | 0.29 | 0.36 | 0.40 | 0.38 | 0.31 | 0.47 | 0.31 | 0.29 | 0.48 | 0.29 | 0.29 | 0.48 | 0.29 | 0.48 | 0.48 | 0.29 | 0.31 | 0.29 | 0.31 | 0.87 | 0.48 | 0.29 | 0.68 | 1.00 | 0.40 | 0.72 |
| S4 | 0.82 | 0.87 | | 0.26 | 0.41 | 0.23 | 0.44 | 0.45 | 0.50 | 0.45 | 0.26 | 0.55 | 0.26 | 0.25 | 0.53 | 0.26 | 0.56 | 0.54 | 0.26 | 0.44 | 0.26 | 0.44 | 0.81 | 0.56 | 0.26 | 0.70 | 0.97 | 0.23 | 0.68 |
| S5 | 0.62 | 1.11 | 1.04 | | 0.00 | 0.00 | 0.00 | 0.49 | 1.16 | 0.49 | 1.00 | 1.10 | 1.00 | 0.99 | 1.12 | 1.00 | 1.07 | 1.11 | 1.00 | 0.49 | 1.00 | 0.49 | 1.13 | 1.06 | 1.00 | 0.56 | 0.91 | 0.00 | 0.49 |
| S6 | 0.62 | 0.61 | 0.74 | 0.00 | | 0.30 | 1.00 | 0.17 | 0.13 | 0.18 | 0.00 | 0.15 | 0.00 | 0.00 | 0.15 | 0.00 | 0.17 | 0.16 | 0.00 | 0.19 | 0.00 | 0.19 | 0.48 | 0.18 | 0.00 | 0.47 | 0.99 | 0.32 | 0.54 |
| S8 | 0.70 | 1.05 | 0.64 | 0.00 | 0.46 | | 0.49 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.88 | 0.00 | 0.00 | 0.80 | 1.10 | 1.01 | 1.00 |
| S9 | 0.62 | 0.61 | 0.74 | 0.00 | 0.94 | 0.30 | | 0.16 | 0.12 | 0.18 | 0.00 | 0.15 | 0.00 | 0.00 | 0.14 | 0.00 | 0.17 | 0.16 | 0.00 | 0.19 | 0.00 | 0.19 | 0.46 | 0.18 | 0.00 | 0.45 | 1.00 | 0.31 | 0.51 |
| S10 | 0.86 | 0.82 | 1.23 | 0.33 | 0.25 | 0.00 | 0.27 | | 0.77 | 1.00 | 0.31 | 0.90 | 0.32 | 0.30 | 0.86 | 0.33 | 0.95 | 0.91 | 0.33 | 1.00 | 0.33 | 1.00 | 1.03 | 0.97 | 0.31 | 1.15 | 0.91 | 0.00 | 1.00 |
| S11 | 0.72 | 0.99 | 1.11 | 0.63 | 0.15 | 0.00 | 0.16 | 0.62 | | 0.63 | 0.64 | 1.02 | 0.63 | 0.64 | 1.02 | 0.63 | 1.02 | 1.02 | 0.63 | 0.63 | 0.63 | 0.63 | 1.09 | 1.02 | 0.64 | 0.72 | 0.92 | 0.00 | 0.63 |
| S13 | 0.85 | 0.82 | 1.21 | 0.33 | 0.27 | 0.00 | 0.29 | 0.99 | 0.77 | | 0.31 | 0.90 | 0.32 | 0.30 | 0.85 | 0.33 | 0.95 | 0.91 | 0.32 | 1.00 | 0.33 | 1.00 | 1.03 | 0.97 | 0.31 | 1.14 | 0.91 | 0.00 | 1.00 |
| S14 | 0.61 | 1.12 | 1.04 | 1.00 | 0.00 | 0.00 | 0.00 | 0.46 | 1.17 | 0.47 | | 1.11 | 1.00 | 1.00 | 1.13 | 1.00 | 1.07 | 1.11 | 1.00 | 0.47 | 1.00 | 0.47 | 1.14 | 1.06 | 1.00 | 0.53 | 0.92 | 0.00 | 0.47 |
| S15 | 0.75 | 0.96 | 1.13 | 0.57 | 0.18 | 0.00 | 0.19 | 0.68 | 0.96 | 0.69 | 0.57 | | 0.57 | 0.57 | 0.99 | 0.57 | 1.01 | 1.00 | 0.57 | 0.69 | 0.57 | 0.69 | 1.08 | 1.01 | 0.57 | 0.79 | 0.92 | 0.00 | 0.69 |
| S18 | 0.62 | 1.11 | 1.04 | 1.00 | 0.00 | 0.00 | 0.00 | 0.48 | 1.16 | 0.48 | 1.00 | 1.10 | | 0.99 | 1.12 | 1.00 | 1.07 | 1.11 | 1.00 | 0.48 | 1.00 | 0.48 | 1.13 | 1.06 | 1.00 | 0.55 | 0.91 | 0.00 | 0.48 |
| S22 | 0.61 | 1.12 | 1.03 | 1.00 | 0.00 | 0.00 | 0.00 | 0.45 | 1.17 | 0.45 | 1.00 | 1.11 | 1.00 | | 1.13 | 1.00 | 1.07 | 1.11 | 1.00 | 0.45 | 1.00 | 0.45 | 1.14 | 1.06 | 1.00 | 0.52 | 0.92 | 0.00 | 0.45 |
| S23 | 0.74 | 0.97 | 1.13 | 0.58 | 0.17 | 0.00 | 0.18 | 0.66 | 0.97 | 0.67 | 0.59 | 1.01 | 0.59 | 0.59 | | 0.58 | 1.01 | 1.01 | 0.59 | 0.67 | 0.58 | 0.67 | 1.09 | 1.01 | 0.59 | 0.76 | 0.92 | 0.00 | 0.67 |
| S24 | 0.62 | 1.11 | 1.04 | 1.00 | 0.00 | 0.00 | 0.00 | 0.49 | 1.16 | 0.49 | 1.00 | 1.10 | 1.00 | 0.99 | 1.12 | | 1.07 | 1.11 | 1.00 | 0.49 | 1.00 | 0.49 | 1.13 | 1.06 | 1.00 | 0.56 | 0.91 | 0.00 | 0.49 |
| S25 | 0.76 | 0.95 | 1.14 | 0.54 | 0.19 | 0.00 | 0.20 | 0.71 | 0.94 | 0.72 | 0.54 | 0.99 | 0.54 | 0.54 | 0.98 | 0.54 | | 0.99 | 0.54 | 0.72 | 0.54 | 0.72 | 1.08 | 1.00 | 0.54 | 0.82 | 0.91 | 0.00 | 0.72 |
| S26 | 0.75 | 0.96 | 1.12 | 0.57 | 0.19 | 0.00 | 0.20 | 0.68 | 0.96 | 0.69 | 0.57 | 1.00 | 0.57 | 0.56 | 0.99 | 0.57 | 1.00 | | 0.57 | 0.69 | 0.57 | 0.69 | 1.08 | 1.01 | 0.57 | 0.79 | 0.92 | 0.00 | 0.69 |
| S27 | 0.62 | 1.11 | 1.04 | 1.00 | 0.00 | 0.00 | 0.00 | 0.48 | 1.16 | 0.48 | 1.00 | 1.10 | 1.00 | 0.99 | 1.12 | 1.00 | 1.07 | 1.11 | | 0.49 | 1.00 | 0.49 | 1.13 | 1.06 | 1.00 | 0.55 | 0.91 | 0.00 | 0.49 |
| S28 | 0.85 | 0.82 | 1.20 | 0.33 | 0.29 | 0.00 | 0.30 | 0.99 | 0.77 | 1.00 | 0.31 | 0.90 | 0.32 | 0.30 | 0.85 | 0.33 | 0.95 | 0.90 | 0.32 | | 0.33 | 1.00 | 1.03 | 0.96 | 0.31 | 1.14 | 0.91 | 0.00 | 1.00 |
| S29 | 0.62 | 1.11 | 1.04 | 1.00 | 0.00 | 0.00 | 0.00 | 0.49 | 1.15 | 0.49 | 1.00 | 1.10 | 1.00 | 0.99 | 1.12 | 1.00 | 1.07 | 1.11 | 1.00 | 0.49 | | 0.49 | 1.13 | 1.06 | 1.00 | 0.56 | 0.91 | 0.00 | 0.49 |
| S30 | 0.85 | 0.82 | 1.20 | 0.33 | 0.29 | 0.00 | 0.30 | 0.99 | 0.77 | 1.00 | 0.31 | 0.90 | 0.32 | 0.30 | 0.85 | 0.33 | 0.95 | 0.90 | 0.32 | 1.00 | 0.33 | | 1.03 | 0.96 | 0.31 | 1.14 | 0.91 | 0.00 | 1.00 |
| S33 | 0.74 | 0.98 | 0.95 | 0.33 | 0.31 | 0.38 | 0.32 | 0.44 | 0.58 | 0.45 | 0.33 | 0.61 | 0.33 | 0.33 | 0.60 | 0.33 | 0.62 | 0.61 | 0.33 | 0.45 | 0.33 | 0.45 | | 0.62 | 0.33 | 0.81 | 0.98 | 0.38 | 0.83 |
| S34 | 0.76 | 0.94 | 1.13 | 0.53 | 0.20 | 0.00 | 0.22 | 0.72 | 0.93 | 0.72 | 0.53 | 0.98 | 0.53 | 0.53 | 0.97 | 0.53 | 1.00 | 0.99 | 0.53 | 0.73 | 0.53 | 0.73 | 1.07 | | 0.53 | 0.82 | 0.91 | 0.00 | 0.73 |
| S35 | 0.61 | 1.12 | 1.04 | 1.00 | 0.00 | 0.00 | 0.00 | 0.46 | 1.17 | 0.47 | 1.00 | 1.11 | 1.00 | 1.00 | 1.13 | 1.00 | 1.07 | 1.11 | 1.00 | 0.47 | 1.00 | 0.47 | 1.14 | 1.06 | | 0.53 | 0.92 | 0.00 | 0.47 |
| S37 | 0.79 | 0.91 | 0.98 | 0.19 | 0.36 | 0.41 | 0.37 | 0.59 | 0.45 | 0.59 | 0.18 | 0.53 | 0.19 | 0.18 | 0.50 | 0.19 | 0.56 | 0.53 | 0.19 | 0.59 | 0.19 | 0.59 | 0.97 | 0.57 | 0.18 | | 0.98 | 0.41 | 1.00 |
| S38 | 0.76 | 0.87 | 0.88 | 0.20 | 0.50 | 0.36 | 0.54 | 0.30 | 0.37 | 0.30 | 0.20 | 0.40 | 0.20 | 0.20 | 0.39 | 0.20 | 0.41 | 0.40 | 0.20 | 0.30 | 0.20 | 0.30 | 0.76 | 0.41 | 0.20 | 0.64 | | 0.37 | 0.67 |
| S39 | 0.70 | 1.04 | 0.63 | 0.00 | 0.49 | 0.99 | 0.50 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.88 | 0.00 | 0.00 | 0.80 | 1.10 | | 1.00 |
| S41 | 0.77 | 0.93 | 0.91 | 0.16 | 0.40 | 0.49 | 0.41 | 0.49 | 0.38 | 0.50 | 0.16 | 0.45 | 0.16 | 0.15 | 0.42 | 0.16 | 0.47 | 0.45 | 0.16 | 0.50 | 0.16 | 0.50 | 0.95 | 0.48 | 0.15 | 0.96 | 1.00 | 0.50 | |

Note: S1–S41 indicate plant species.

**Table S3** Coefficient of niche overlap in no mound

| No. | S1 | S2 | S4 | S5 | S6 | S7 | S8 | S9 | S10 | S11 | S12 | S14 | S15 | S16 | S19 | S20 | S21 | S22 | S23 | S24 | S25 | S26 | S27 | S28 | S29 | S30 | S31 | S32 | S33 | S34 | S35 | S37 | S40 | S41 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S1 | | 0.42 | 0.42 | 0.84 | 0.43 | 0.62 | 0.58 | 0.83 | 0.65 | 0.87 | 0.84 | 0.85 | 0.92 | 0.53 | 0.54 | 0.72 | 0.42 | 0.84 | 0.69 | 0.54 | 0.42 | 0.90 | 0.94 | 0.42 | 0.72 | 0.80 | 0.85 | 0.44 | 0.69 | 0.53 | 0.42 | 0.53 | 0.54 | 0.66 |
| S2 | 0.98 | | 1.00 | 0.91 | 0.25 | 0.64 | 1.16 | 0.58 | 0.81 | 0.67 | 1.03 | 0.55 | 0.82 | 0.54 | 0.57 | 0.94 | 1.00 | 0.96 | 0.86 | 0.60 | 1.00 | 0.79 | 0.85 | 1.00 | 0.88 | 0.48 | 0.58 | 0.28 | 0.92 | 0.52 | 1.00 | 0.54 | 0.56 | 0.89 |
| S4 | 0.98 | 1.00 | | 0.91 | 0.25 | 0.64 | 1.16 | 0.58 | 0.81 | 0.67 | 1.03 | 0.55 | 0.82 | 0.54 | 0.57 | 0.94 | 1.00 | 0.96 | 0.86 | 0.60 | 1.00 | 0.79 | 0.85 | 1.00 | 0.88 | 0.48 | 0.58 | 0.28 | 0.92 | 0.52 | 1.00 | 0.54 | 0.56 | 0.89 |
| S5 | 0.75 | 0.35 | 0.35 | | 0.21 | 0.61 | 0.64 | 0.88 | 0.68 | 0.96 | 0.98 | 0.86 | 0.93 | 0.53 | 0.53 | 0.45 | 0.35 | 1.00 | 0.67 | 0.54 | 0.35 | 0.90 | 0.99 | 0.35 | 0.44 | 0.81 | 0.64 | 0.22 | 0.65 | 0.53 | 0.35 | 0.54 | 0.53 | 0.69 |
| S6 | 1.02 | 0.25 | 0.25 | 0.56 | | 1.04 | 0.46 | 0.75 | 0.96 | 0.78 | 0.54 | 1.02 | 1.01 | 0.24 | 0.26 | 1.04 | 0.26 | 0.57 | 1.01 | 0.27 | 0.27 | 1.07 | 0.92 | 0.27 | 1.07 | 1.07 | 1.00 | 1.00 | 0.24 | 0.24 | 0.27 | 0.25 | 0.25 | 0.92 |
| S7 | 0.67 | 0.29 | 0.29 | 0.74 | 0.48 | | 0.68 | 0.72 | 1.01 | 0.88 | 0.78 | 0.90 | 1.04 | 0.18 | 0.19 | 0.66 | 0.29 | 0.78 | 1.01 | 0.20 | 0.30 | 1.04 | 0.99 | 0.30 | 0.67 | 0.95 | 0.56 | 0.48 | 0.27 | 0.17 | 0.30 | 0.18 | 0.18 | 1.00 |
| S8 | 0.75 | 0.64 | 0.64 | 0.91 | 0.25 | 0.81 | | 0.63 | 0.93 | 0.80 | 1.00 | 0.68 | 0.94 | 0.31 | 0.34 | 0.72 | 0.64 | 0.97 | 0.94 | 0.35 | 0.63 | 0.90 | 0.94 | 0.63 | 0.69 | 0.68 | 0.46 | 0.27 | 0.59 | 0.31 | 0.63 | 0.32 | 0.33 | 0.96 |
| S9 | 0.77 | 0.23 | 0.23 | 0.92 | 0.30 | 0.62 | 0.46 | | 0.65 | 0.99 | 0.86 | 1.00 | 0.94 | 0.59 | 0.60 | 0.44 | 0.23 | 0.90 | 0.64 | 0.60 | 0.24 | 0.93 | 1.00 | 0.24 | 0.44 | 0.94 | 0.79 | 0.30 | 0.59 | 0.59 | 0.24 | 0.60 | 0.60 | 0.65 |
| S10 | 0.66 | 0.35 | 0.35 | 0.77 | 0.42 | 0.96 | 0.74 | 0.71 | | 0.88 | 0.82 | 0.86 | 1.03 | 0.20 | 0.22 | 0.65 | 0.35 | 0.82 | 1.00 | 0.23 | 0.36 | 1.03 | 0.99 | 0.36 | 0.65 | 0.91 | 0.53 | 0.42 | 0.33 | 0.20 | 0.35 | 0.21 | 0.21 | 1.00 |
| S11 | 0.72 | 0.24 | 0.24 | 0.89 | 0.27 | 0.67 | 0.52 | 0.89 | 0.71 | | 0.89 | 0.92 | 0.98 | 0.47 | 0.47 | 0.43 | 0.24 | 0.91 | 0.71 | 0.46 | 0.24 | 0.96 | 1.01 | 0.24 | 0.43 | 0.90 | 0.66 | 0.28 | 0.54 | 0.47 | 0.24 | 0.47 | 0.47 | 0.71 |
| S12 | 0.74 | 0.39 | 0.39 | 0.97 | 0.20 | 0.64 | 0.69 | 0.82 | 0.71 | 0.95 | | 0.82 | 0.94 | 0.48 | 0.48 | 0.48 | 0.39 | 1.00 | 0.71 | 0.48 | 0.39 | 0.91 | 0.99 | 0.39 | 0.46 | 0.78 | 0.59 | 0.21 | 0.64 | 0.48 | 0.39 | 0.48 | 0.48 | 0.74 |
| S14 | 0.75 | 0.21 | 0.21 | 0.84 | 0.38 | 0.73 | 0.47 | 0.94 | 0.74 | 0.98 | 0.81 | | 0.97 | 0.49 | 0.49 | 0.50 | 0.21 | 0.85 | 0.74 | 0.49 | 0.22 | 0.98 | 1.00 | 0.22 | 0.50 | 0.98 | 0.76 | 0.38 | 0.48 | 0.49 | 0.22 | 0.49 | 0.49 | 0.73 |
| S15 | 0.73 | 0.28 | 0.28 | 0.83 | 0.34 | 0.77 | 0.58 | 0.81 | 0.80 | 0.95 | 0.85 | 0.89 | | 0.36 | 0.37 | 0.54 | 0.28 | 0.86 | 0.81 | 0.37 | 0.28 | 0.99 | 1.00 | 0.28 | 0.54 | 0.89 | 0.62 | 0.34 | 0.47 | 0.36 | 0.28 | 0.36 | 0.37 | 0.80 |
| S16 | 0.94 | 0.40 | 0.40 | 1.04 | 0.18 | 0.29 | 0.43 | 1.13 | 0.35 | 1.01 | 0.96 | 0.98 | 0.81 | | 1.00 | 0.41 | 0.42 | 1.01 | 0.36 | 1.00 | 0.43 | 0.79 | 0.95 | 0.43 | 0.38 | 0.82 | 0.99 | 0.20 | 0.99 | 1.00 | 0.42 | 1.00 | 1.00 | 0.39 |
| S19 | 0.94 | 0.43 | 0.43 | 1.04 | 0.20 | 0.31 | 0.46 | 1.12 | 0.37 | 0.99 | 0.96 | 0.98 | 0.80 | 0.99 | | 0.43 | 0.44 | 1.01 | 0.38 | 1.00 | 0.45 | 0.79 | 0.95 | 0.45 | 0.41 | 0.82 | 0.99 | 0.22 | 0.99 | 0.99 | 0.45 | 0.99 | 1.00 | 0.41 |
| S20 | 1.01 | 0.56 | 0.56 | 0.71 | 0.62 | 0.86 | 0.79 | 0.66 | 0.90 | 0.73 | 0.76 | 0.79 | 0.94 | 0.32 | 0.34 | | 0.57 | 0.74 | 0.95 | 0.36 | 0.57 | 0.95 | 0.89 | 0.57 | 0.99 | 0.79 | 0.79 | 0.62 | 0.52 | 0.31 | 0.57 | 0.33 | 0.33 | 0.91 |
| S21 | 0.98 | 1.00 | 1.00 | 0.91 | 0.26 | 0.64 | 1.16 | 0.59 | 0.81 | 0.68 | 1.02 | 0.57 | 0.82 | 0.55 | 0.59 | 0.94 | | 0.96 | 0.86 | 0.61 | 1.00 | 0.79 | 0.84 | 1.00 | 0.88 | 0.49 | 0.60 | 0.29 | 0.92 | 0.53 | 1.00 | 0.56 | 0.57 | 0.89 |
| S22 | 0.74 | 0.36 | 0.36 | 0.98 | 0.21 | 0.63 | 0.66 | 0.85 | 0.70 | 0.96 | 0.99 | 0.85 | 0.94 | 0.50 | 0.50 | 0.46 | 0.36 | | 0.70 | 0.50 | 0.36 | 0.91 | 0.99 | 0.36 | 0.44 | 0.81 | 0.61 | 0.22 | 0.63 | 0.50 | 0.36 | 0.50 | 0.50 | 0.72 |
| S23 | 0.69 | 0.37 | 0.37 | 0.76 | 0.43 | 0.95 | 0.74 | 0.70 | 0.99 | 0.87 | 0.81 | 0.85 | 1.02 | 0.21 | 0.22 | 0.68 | 0.37 | 0.81 | | 0.23 | 0.37 | 1.03 | 0.98 | 0.37 | 0.68 | 0.90 | 0.55 | 0.43 | 0.34 | 0.20 | 0.37 | 0.21 | 0.22 | 0.99 |
| S24 | 0.94 | 0.44 | 0.44 | 1.04 | 0.20 | 0.32 | 0.48 | 1.12 | 0.39 | 0.98 | 0.95 | 0.98 | 0.80 | 0.98 | 1.00 | 0.45 | 0.46 | 1.00 | 0.40 | | 0.47 | 0.79 | 0.94 | 0.47 | 0.42 | 0.82 | 0.99 | 0.22 | 0.98 | 0.98 | 0.46 | 0.99 | 0.99 | 0.43 |
| S25 | 0.97 | 0.99 | 0.99 | 0.91 | 0.27 | 0.64 | 1.15 | 0.60 | 0.81 | 0.68 | 1.02 | 0.58 | 0.81 | 0.56 | 0.60 | 0.94 | 1.00 | 0.96 | 0.85 | 0.62 | | 0.79 | 0.84 | 1.00 | 0.88 | 0.51 | 0.61 | 0.30 | 0.92 | 0.55 | 1.00 | 0.57 | 0.58 | 0.89 |
| S26 | 0.73 | 0.27 | 0.27 | 0.81 | 0.37 | 0.78 | 0.57 | 0.82 | 0.82 | 0.94 | 0.83 | 0.90 | 1.00 | 0.36 | 0.36 | 0.55 | 0.27 | 0.84 | 0.82 | 0.37 | 0.27 | | 1.00 | 0.27 | 0.55 | 0.91 | 0.64 | 0.37 | 0.45 | 0.36 | 0.27 | 0.36 | 0.36 | 0.82 |
| S27 | 0.74 | 0.28 | 0.28 | 0.87 | 0.31 | 0.72 | 0.57 | 0.85 | 0.76 | 0.96 | 0.88 | 0.90 | 0.98 | 0.42 | 0.43 | 0.50 | 0.28 | 0.89 | 0.76 | 0.42 | 0.28 | 0.96 | | 0.29 | 0.50 | 0.88 | 0.64 | 0.31 | 0.52 | 0.42 | 0.28 | 0.42 | 0.43 | 0.76 |
| S28 | 0.97 | 0.99 | 0.99 | 0.91 | 0.27 | 0.64 | 1.15 | 0.61 | 0.81 | 0.68 | 1.02 | 0.58 | 0.81 | 0.56 | 0.60 | 0.94 | 1.00 | 0.96 | 0.85 | 0.63 | 1.00 | 0.79 | 0.84 | | 0.88 | 0.51 | 0.61 | 0.30 | 0.92 | 0.55 | 1.00 | 0.57 | 0.59 | 0.89 |
| S29 | 1.02 | 0.53 | 0.53 | 0.69 | 0.65 | 0.88 | 0.76 | 0.67 | 0.90 | 0.74 | 0.74 | 0.81 | 0.95 | 0.31 | 0.33 | 1.00 | 0.53 | 0.72 | 0.96 | 0.34 | 0.54 | 0.96 | 0.90 | 0.54 | | 0.82 | 0.81 | 0.65 | 0.49 | 0.30 | 0.54 | 0.31 | 0.32 | 0.91 |
| S30 | 0.72 | 0.18 | 0.18 | 0.81 | 0.41 | 0.79 | 0.47 | 0.91 | 0.79 | 0.97 | 0.79 | 1.00 | 1.00 | 0.42 | 0.42 | 0.51 | 0.19 | 0.83 | 0.79 | 0.42 | 0.19 | 1.01 | 1.01 | 0.20 | 0.52 | | 0.72 | 0.41 | 0.41 | 0.42 | 0.19 | 0.42 | 0.42 | 0.78 |
| S31 | 0.98 | 0.29 | 0.29 | 0.84 | 0.50 | 0.60 | 0.42 | 0.99 | 0.60 | 0.92 | 0.77 | 1.01 | 0.90 | 0.65 | 0.66 | 0.66 | 0.30 | 0.82 | 0.63 | 0.66 | 0.30 | 0.91 | 0.95 | 0.31 | 0.66 | 0.94 | | 0.50 | 0.65 | 0.65 | 0.30 | 0.65 | 0.65 | 0.60 |
| S32 | 1.02 | 0.28 | 0.28 | 0.58 | 0.99 | 1.03 | 0.48 | 0.75 | 0.96 | 0.77 | 0.56 | 1.01 | 1.00 | 0.27 | 0.29 | 1.03 | 0.29 | 0.59 | 1.00 | 0.30 | 0.30 | 1.05 | 0.92 | 0.30 | 1.07 | 1.06 | 1.00 | | 0.26 | 0.26 | 0.29 | 0.27 | 0.28 | 0.92 |
| S33 | 0.97 | 0.55 | 0.55 | 1.02 | 0.14 | 0.35 | 0.64 | 0.89 | 0.45 | 0.93 | 1.02 | 0.78 | 0.84 | 0.79 | 0.80 | 0.52 | 0.56 | 1.02 | 0.48 | 0.79 | 0.56 | 0.79 | 0.94 | 0.56 | 0.49 | 0.65 | 0.78 | 0.16 | | 0.79 | 0.56 | 0.79 | 0.80 | 0.49 |
| S34 | 0.94 | 0.39 | 0.39 | 1.05 | 0.18 | 0.28 | 0.42 | 1.13 | 0.34 | 1.01 | 0.96 | 0.98 | 0.81 | 1.00 | 1.00 | 0.40 | 0.41 | 1.01 | 0.35 | 1.00 | 0.42 | 0.79 | 0.96 | 0.42 | 0.37 | 0.82 | 0.99 | 0.20 | 0.99 | | 0.41 | 1.00 | 1.00 | 0.38 |
| S35 | 0.97 | 0.99 | 0.99 | 0.91 | 0.27 | 0.64 | 1.15 | 0.60 | 0.81 | 0.68 | 1.02 | 0.57 | 0.82 | 0.56 | 0.59 | 0.94 | 1.00 | 0.96 | 0.85 | 0.62 | 1.00 | 0.79 | 0.84 | 1.00 | 0.88 | 0.50 | 0.60 | 0.29 | 0.92 | 0.54 | | 0.56 | 0.58 | 0.89 |
| S37 | 0.94 | 0.41 | 0.41 | 1.05 | 0.18 | 0.29 | 0.44 | 1.14 | 0.36 | 1.00 | 0.96 | 0.98 | 0.80 | 0.99 | 1.00 | 0.41 | 0.42 | 1.01 | 0.37 | 1.00 | 0.43 | 0.79 | 0.95 | 0.43 | 0.39 | 0.82 | 0.99 | 0.20 | 0.99 | 0.99 | 0.43 | | 1.00 | 0.39 |
| S40 | 0.94 | 0.42 | 0.42 | 1.04 | 0.19 | 0.30 | 0.45 | 1.13 | 0.36 | 1.00 | 0.96 | 0.98 | 0.80 | 0.99 | 1.00 | 0.42 | 0.43 | 1.01 | 0.37 | 1.00 | 0.44 | 0.79 | 0.95 | 0.44 | 0.40 | 0.82 | 0.99 | 0.21 | 0.99 | 0.99 | 0.43 | 1.00 | | 0.40 |
| S41 | 0.67 | 0.38 | 0.38 | 0.78 | 0.40 | 0.94 | 0.76 | 0.71 | 0.99 | 0.87 | 0.84 | 0.85 | 1.02 | 0.22 | 0.24 | 0.66 | 0.38 | 0.84 | 1.00 | 0.25 | 0.39 | 1.02 | 0.98 | 0.39 | 0.65 | 0.89 | 0.52 | 0.40 | 0.35 | 0.22 | 0.39 | 0.23 | 0.23 | |

Note: S1–S41 indicate plant species.