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The effect of grazing and reclamation on rodent community stability in the Alxa desert

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Ecosystem stability has been of increasing interest in the past several decades as it helps predict the consequences of anthropogenic disturbances on ecosystems. A wild rodent community under reclamation and different grazing disturbances in the Alxa Desert was investigated using live trapping from 2006 to 2011. We studied the rodent community composition, community diversity, and variability of different life history strategies. These results showed that reclamation reduced rodent community stability by increasing temporal variability of community, reducing rodent community resistance as shown by decreasing dominance of *KSS* strategists, and increased the resistance variability of the rodent community by increasing the variability of abundance and richness for *KSS* strategists. Grazing reduced rodent community resilience by reducing the dominance of *rRF* strategists, and increased the resilience variability of the rodent community by increasing the variability of abundance and richness for *rRF* strategists. Those results may answer the three ecological questions about how ecosystems respond to disturbances from a diversity perspective. The ecosystems with intermediate disturbance are more stable, in other words, with higher resistance and resilience. The increase of *KSS* strategists means the increase of resistance of the community. The increase of *rRF* strategists means the increase of community resilience.

KEYWORDS

life history strategies, community stability, diversity, resistance, resilience, rodent

1. Introduction

Disturbances are an essential component of desert ecosystems. While they play an important role in desert renewal and diversification, disturbances can generate profound changes in desert composition and structure. With the global environmental change, the occurrence and severity of biotic and abiotic disturbances have increased, affecting desert ecosystems around the world (Grimm and Fisher, 1989; Frank et al., 2013). Such alterations in disturbance regimes may change desert responses to disturbances, resulting in altered ecosystems and affecting their function and provision of services (Eldridge et al., 2009; Quoreshi et al., 2019). The concept of ecological disturbance originated from ecological studies at the community level, and the influence of interference on this scale was obvious. Many species groups are closely related to the disturbance, and one prominent function of the disturbance is to lead to the change of various

resources in the ecosystem and the reorganization of the ecosystem structure leading to the formation of heterogeneous environment (Chen and Fu, 2000). Two major foci of ecological research involve reciprocal views of the relationship between biodiversity and disturbance: Disturbance determines community diversity or diversity determines realized disturbance severity. A largely separate body of ecological research has examined how biodiversity affects community or ecosystem properties. Experimental explorations of the biodiversity–stability relationship often focus on the effect of diversity on community response to specific disturbance events, revealing several sound theoretical and biological mechanisms by which diversity might influence the magnitude of loss to (resistance) or rate of recovery from (resilience) disturbance (Sánchez-Pinillos et al., 2019).

Understanding desert responses to disturbances requires considering the mechanisms that enhance ecosystems to persist through time around an equilibrium state subjected to disturbances (Scheffer et al., 2012; Willis et al., 2018). Several studies recognize the important insights gained by considering resistance and resilience as related but distinct measurable components of ecosystem responses to disturbances (Hodgson et al., 2015; Nimmo et al., 2015). Resistance can be defined as the ability of ecological systems to persist through the disturbance event (Tilman and Downing, 1994; Connell and Ghedini, 2015), while resilience is the ecosystem's capacity to recover or “bounce back” after the disturbance has been alleviated (Gunderson, 2000). Given the variety of meanings around these broad concepts, it is important to establish procedures to specifically measure these two properties when assessing responses of natural communities to disturbances (Hodgson et al., 2015; Nimmo et al., 2015). The resistance of an ecosystem to a given disturbance can be measured by the change in ecosystem structure and composition caused by the disturbance agent and can be estimated by comparing ecosystem characteristics before and immediately after the disturbance. Measuring resilience requires considering changes over a longer post-disturbance period to evaluate the degree to which an ecosystem returns to pre-disturbance conditions (Díaz-Delgado et al., 2002; Bagchi et al., 2017).

Desert resistance and resilience to disturbances depend on multiple variables acting at different levels of organization. Species responses to disturbances mediate changes in their abundance, affecting the composition and structure of the entire community, and therefore, forest functioning as well (Oliver et al., 2015). Different quantitative indices have been successfully applied to identify such variables and to compare forests based on their species responses (Bruehlheide and Luginbuhl, 2009; Sánchez-Pinillos et al., 2019). While useful, the simplification inherent in quantitative, univariate indices does not capture the complexity of the entire system (Quinlan et al., 2016). Further insights into desert resistance and resilience can be gained by combining quantitative indicators based on cross-scale temporal dynamics with descriptive analyses of post-disturbance ecosystem-level variants. This approach allows us to comprehensively compare the responses of desert while assessing potential factors affecting resistance and resilience.

Stability may be caused in two ways: through the pattern of interaction between species in the community, or through the inherent stability of the species (MacArthur, 1955). Much subsequent research focused on the first pathway, namely the relationship between diversity and stability as well as the interaction between species (Hairston et al., 1968; Pimm, 1984), while less research has focused on the inherent stability of species. McCann (2000)

suggested that the ability of a community to accommodate species or functional groups with different responsiveness limits stability. Functional and compositional stabilities were two aspects of stability in ecological communities (Huelsmann and Ackermann, 2022). In previous studies, life history characteristics are often used as the main indicators of community functional (Kirwan et al., 2009; Rodríguez and Ojeda, 2014; Lin et al., 2022). Life history theory (Stearns, 1992) predicts that certain environments favor specific suites of traits. Species with different life history strategies take different behavioral responses to environmental changes, which can adapt quickly to environmental changes to survive. While other species have taken non-adaptive responses to human disturbances which not encountered in their evolutionary history (Ghalambor et al., 2007). Reducing population density or lead to extinction in non-suitable habitats by emigration or death (Badyaev, 2005), and non-adaptive responses leading to changes in species distribution, diversity and community patterns (Tuomainen and Candolin, 2011). MacArthur and Wilson (1967) introduced *r*-*K* theory to account for linkages between life history strategies and specific environmental conditions. The *r*-*K* model suggests that life history strategies represent a continuum bounded by two end points: The *r*-strategy, characteristic of small, high-fecundity animals, and the *K* strategy, characteristic of large, low-fecundity animals. The model implies moving from disturbed environments. The increase in *K* strategists in a community imply an increase in community resistance, whereas an increase in *r* strategists implies an increase in community resilience (Lepš et al., 1982). Studying how different systems are dominated by animals with different life history strategies can help us solve the problem of resistance and resilience (Pimm, 1984).

Alxa desert is located in the Gobi and Karakum regions of Asia. It is an interior continental desert far away from the ocean and receiving air that has been depleted of moisture. This desert and the Great Basin of North America exemplify interior continental deserts (Kelt, 2011). In the 1990s, a large agricultural population migrated to the Alxa desert. With the increase in the agricultural population, land reclamation and heavy grazing became the main human disturbances affecting this desert ecosystem. Rodents are an important part of the environment, and an important indicator of environmental change in desert ecosystems (Jones and Longland, 1999; Flowerdew et al., 2004). Studies of rodents have contributed significantly to the development of desert ecology theory and to understanding animal adaptation to arid environments (Ojeda and Tabeni, 2009). Understanding the mechanisms involved in rodent community stability has great significance for further evaluation of the stability of desert ecosystems subjected to human disturbance. However, studies on Chinese desert rodent community stability are not common.

In this study, based on Pianka's classification principle for *r* and *K* strategists (Pianka, 1970) and Harvey' classification principle (Read and Harvey, 2009) for fast-slow life history strategies, we further divided rodents into different life history strategies. Then we adapted a method of measuring and assessing ecosystem resistance and resilience to disturbances by comparing species composition and structure among different strategies, combining dissimilarity indices from ecosystem composition and structure with variability analyses of these descriptors in different disturbances. This method can help to answer three questions considered essential in the understanding of ecosystem responses to disturbances (see for example Willis et al., 2018): (i) Which types of ecosystems are the most resistance and resilience (ii), what factors contribute to resistance and resilience, or

(iii) how prone is an ecosystem to losing resilience? In this article, we evaluate rodent community stability subjected to different grazing patterns and to land reclamation in the Alxa desert, investigating species diversity, resilience, resistance, and variability of the rodent community. Specifically, we assume that: (1) Land reclamation and heavy grazing would decrease rodent community stability by reducing rodent community diversity; and (2) Land reclamation and grazing change resilience, resistance or variability of the desert rodent community by regulating the composition of different bionomic strategists in the community.

2. Materials and methods

2.1. Study site

This study was conducted in the southern part of Alxa Zuo Qi at the eastern edge of the Tengger Desert, Inner Mongolia, China (E104°10′–105°30′, N37°24′–38°25′), from April to October each year between 2006 and 2011. Our study area has a continental climate with cold and dry winters and warm summers. Annual temperatures range from –36 to 42°C with a mean of 8.3°C. Annual precipitation ranges from 45 to 215 mm, but about 70 percent falls from June to September. Potential evaporation ranges from 3,000 to 4,700 mm, and the annual frost-free period is 156 days. Approximately 5–15% of the ground is covered with shrubs, forbs, and some gramineous plants. Shrubs mainly consist of *Zygophyllum xanthoxylon*, *Nitraria tangutorum*, *Caragana brachypoda*, *Ceratoides latens*, *Oxytropis aciphylla*, *Artemisia sphaerocephala*, and *Artemisia xerophytica* with *Reaumuria soongorica* as the dominant species. The major grasses/forbs species are *Cleistogenes squarosa*, *Peganum nigellastrum*, *Cynanchum komarovii*, *Salsola pestifer*, *Suaeda glauca*, *Bassia dasyphylla*, *Corispermum mongolicum*, *Artemisia dubia*, and *Plantago lessingii* (Yuan et al., 2018).

2.2. Methods

The experiment, established in 2006, adopted a randomized block design with three blocks and four treatments, including light sheep grazing, heavy sheep grazing, grazing exclusion and land reclamation, to assess the effect livestock grazing and agricultural reclamation on small mammal communities. Each block encompassed 240 ha and each treatment unit was 60 ha. The two grazing treatments and grazing exclusion were established with standard sheep fencing (110 cm high). In the light grazing sites, sheep grazing intensity was controlled within the range of 0.83–1.00 sheep per ha. In the heavy grazing sites, sheep grazing intensity was controlled within the range of 3.75–4.23 sheep per ha. This was close to the common grazing intensity in the study area, but significantly higher than the Inner Mongolia government standards, which ranged from 0.603 to 1.120 sheep per ha in the study area. The land reclamation plots previously had plant species similar to the grazing exclusion plots, but were reclaimed in 1994 by planting saxaul (*Haloxylon ammodendron*), sunflowers (*Helianthus annuus*), and maize (*Zea mays*). A 7 × 8 trapping grid (0.96 ha) at a 15 m inter-trap distance was established at the center of each treatment unit. Twelve trapping grids were established in the study area. One wire-mesh live trap (42 cm × 17 cm × 13 cm) was placed at each trap station.

2.3. Trapping of rodents

Rodents were live trapped for four consecutive days at 4-week intervals from April 2006 to October 2011. Trapping was not run during winter (from November to March). Traps were baited with fresh peanuts, and checked twice (morning and afternoon) each day. Considering that the average survival time of jerboa was greater than that of other non-jerboa species in our study areas. The life span of jerboa is longer than 2 years, and the average life span of non-jerboa species is shorter than 2 years. The electronic chips be used have a life span of 2 years. Each captured jerboa individual was sexed, marked with a 1.5 g aluminum leg ring (0.4 cm diameter) with a unique identification number (ID) attached to the left hind foot, and weighed to the nearest 1 g. Each captured non-jerboa individual was sexed, marked with a electronic chip with a unique identification number (ID). The sex, capture station, body mass, and reproductive condition of each capture were recorded. Males were considered in reproductive condition if they had scrotal testes. Females were considered reproductive if they possessed enlarged nipples surrounded with white mammary tissue, or a bulging abdomen. In order to avoid accidental death, traps were closed on extremely warm or rainy days, and trapping time was extended after extremely warm or rainy days to ensure 4 days of trapping in each month (Wu et al., 2016).

To assess the effectiveness of the aluminum leg rings, whether the leg rings are lost, we conducted another experiment in 2018 and 2019. In April and May 2018, both the leg rings and electronic chips were used to mark jerboas at the same time, and the loss of the leg rings and electronic chip was recorded in September of the same year. At the beginning of this pre-experiment, we captured and marked 21 Northern three-toed Jerboa (NTJ), *Dipus sagitta* individuals and 15 Mongolian five-toed Jerboa (MFJ), *Orientalactaga sibirica* individuals in 2018. In September of 2019, six NTJ marked individuals and seven MFJ marked individuals were recaptured. And there was no loss of leg rings or chips.

In this study we calculated population abundance of rodent with a minimum number known to be alive (MNA) (Krebs, 1966; Hilborn et al., 1976).

Proportion of the i 'th rodent (%)

$$= \frac{\text{The population density of the } i\text{'th species}}{\text{The total density of rodents in a community}} \times 100\%$$

2.4. Vegetation sampling

We conducted vegetation sampling monthly from April 2006 to October 2011. During each month's sampling, we randomly selected three 100-m² plots within each treatment unit to sample shrubs. Within each 100-m² plot, we randomly selected three individuals of small, medium, and large size of each species of shrub present. We removed a tenth of aboveground material (decided by cover) from the three shrubs and airdried samples. We then calculated the biomass of a shrub species using the formula $TB = 10 \times DW \times D/100$, where DW is mean dry weight of 1–10th of aboveground material averaged over the three individuals, D is the density of a shrub species (individuals/100 m²), and TB is total aboveground standing biomass (g/m²) (Yuan et al., 2018).

Within each 100-m² plot, we randomly placed three 1-m² quadrats to sample grasses and forbs. We clipped aboveground plant

TABLE 1 Biological features of captured rodent species in different treatments in Alxa desert, Inner Mongolia, China, from April 2006 to October 2011.

| Species | Body length c (mm) | Body mass (g) | Births number (birth/year) | Litter size | Pregnancy (day) | Reproductive period (month) | Longevity (month) | Hibernation (yes or no) |
|----------------------------------|--------------------|---------------|----------------------------|-------------|-----------------|-----------------------------|-------------------|-------------------------|
| <i>Spermophilus alaschanicus</i> | 163–230 | 173.7–220.4 | 1 | 4–5 | 28–30 | 2 | About 72 | Yes |
| <i>Orientallactaga sibirica</i> | 112–160 | 72.2–108.9 | 1 | 4–5 | >20 | 3 | >24 | Yes |
| <i>Dipus sagitta</i> | 114–135 | 86.4–95.9 | 1 | 4–6 | 28 | 3 | >24 | Yes |
| <i>Stylodipus andrewsi</i> | 110–136 | 83.1–88.4 | 2 | 2–4 | — | — | >24 | Yes |
| <i>Meriones meridianus</i> | 68–136 | 46.5–64.1 | 2–3 | 6 | 22–28 | 7 | <12 | No |
| <i>Meriones unguiculatus</i> | 90–130 | 46.8–57.5 | 2–3 | 6–7 | 20–25 | 12 | 18–24 | No |
| <i>Cricetulus barabensis</i> | 70–110 | 17.7–25.9 | 4–5 | 4–8 | 22 | 9–10 | About 10 | No |
| <i>Cricetulus eversmanni</i> | 76–180 | 21.0–27.4 | 2–3 | 4–6 | — | 6 | — | No |
| <i>Phodopus roborovskii</i> | 73–75 | 10.37–20.14 | ≥2 | 5–6 | 20–22 | 7 | <24 | No |

“—”: Missing data.

material of grasses and forbs within each 1-m² quadrat. We air-dried all aboveground plant material for >30 days until there were no changes in dry weight. We weighed dry plant material to the nearest 0.01 g to estimate aboveground standing biomass of grasses and forbs with an electronic balance (Model TD5002, Jingnuo, Yuyao, China) (Yuan et al., 2018).

2.5. Community diversity

There is no one indicator that can be used to evaluate stability (Sutherland, 1981; Pimm, 1984). In order to understand the effect of different disturbances on desert rodent community stability, our study analyzed the disturbed rodent community from the aspects of community diversity, variability of species richness and population abundance, community resistance and community resilience.

Species richness, Shannon–Wiener index, Pielou evenness index, and Simpson’s diversity index were calculated by years and treatments. These indices were analyzed using a mixed effects model (Proc mixed, SAS9.2) with a significance level of $\alpha = 0.05$, using Tukey’s test for means comparison. Blocks and years were set as random effects. All values are given as the mean \pm 1 standard error of mean (sem), unless otherwise noted.

2.6. Community resistance and resilience: Segmentation by bionomic strategies

Based on Pianka’s classification principle for *r* and *K* strategists (Pianka, 1970) and Harvey’ classification principle (Read and Harvey, 2009) for fast-slow life history strategies, statistical analysis was applied to six biological indicators, i.e., body length, litters, litter size, pregnancy, reproductive period, and longevity (Zhang and Wang, 1998; Wu et al., 2009; Table 1).

Cluster analysis was performed using the unweighted pair-group method with arithmetic means (due to incomplete data on individual species, pregnancy was not included, Table 1). In high latitude areas, hibernation contributes significantly to the survival rate of species under adverse environmental conditions (Bakran-Lebl et al., 2011; Bieber et al., 2012; Armitage, 2017). Hence, whether a species hibernates or not was added into the classification index (Armitage,

2017). The result of cluster analysis suggested that rodents could be divided into two categories. The Alashan ground squirrel (AGS, *Spermophilus alaschanicus*), MFJ, NTJ, and Mongolian thick-tailed three-toed jerboa (MTTJ, *Stylodipus andrewsi*), with larger body size, long longevity, short reproductive period and relatively weak fecundity, were clustered into one category. We defined this category as *K*-stress tolerant slow strategists (*KSS*). Other rodent species with smaller body size, short longevity, long reproductive period, and high fertility were clustered into the other category, and, were categorized as *r*-ruderal-fast strategists (*rRF*) (Figure 1). According to the classification by bionomic strategy, we calculated the species richness and community structure of rodents with different bionomic strategies in different disturbed habitats. We defined a community with more *KSS* strategists dominance shows greater resistance, while a community with more *rRF* strategists dominance shows greater resilience.

2.7. W-statistic calculation

We also used the *W*-statistic to analyze the dominance of different life strategists in different treatments, using the formula as follows (Clarke, 1990):

$$W = \frac{\sum_{j=1}^S [(\sum_{j=1}^i b_j) - (\sum_{j=1}^i a_j)]}{50(S-1)}$$

Where *S* is the number of species in the community, *b_j* is the cumulative biomass ratio of the *j* species before order by biomass from the highest to the lowest; *a_j* is the cumulative abundance ratio of the *j* species before order by abundance from the highest to the lowest. When *W* is close to 1, the biomass of the community is gradually dominated by a single species, while the abundance of each species tends to be the same. When *W* approaches -1 , the opposite situation is indicated.

Species richness, capture rate, proportion of captured rodents with different bionomic strategies and *W*-values were calculated by years and treatments. These indices were analyzed using a mixed effects model (Proc mixed, SAS9.2) with a significance level of $\alpha = 0.05$, and using Tukey’s test for means comparison. Blocks and years were set as random effects.

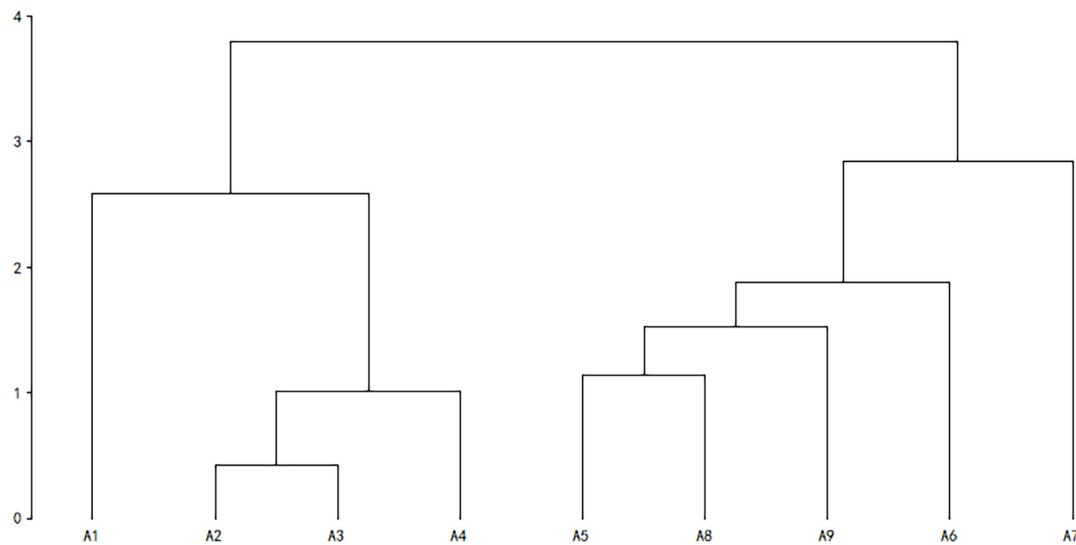


FIGURE 1

Cluster analysis of rodents with different bionomic strategies. Cluster analysis was performed using UPGMA, A1–A9 indicate, respectively: Alashan ground Squirrel (*Spermophilus alaschanicus*), Mongolian five-toed jerboa (*Orientallactaga sibirica*), Northern three-toed jerboa (*Dipus sagitta*), Mongolian thick-tailed three-toed jerboa (*Stylodipus andrewsi*), Midday gerbil (*Meriones meridianus*), Mongolian gerbil (*Meriones unguiculatus*), Chinese hamster (*Cricetulus barabensis*), Eversmann's hamster (*Cricetulus eversmanni*), and Desert hamster (*Phodopus roborovskii*).

2.8. Community variation

The community stability is expressed by temporal variability of community (Thebault and Loreau, 2005). The coefficient of variation (C.V.) is usually taken as an indicator of temporal variability of community (Bai and Chen, 2000; Thebault and Loreau, 2005). Lower temporal variability of community indicates higher community stability (Yang et al., 2022).

$$\text{C.V. (\%)} = \frac{\text{Standard deviation of population abundance or species richness}}{\text{Mean of population abundance or species richness of 6 years}} \times 100\%$$

2.9. Habitat suitability

Habitat suitability was investigated in different treatments. Habitat suitability refers to the possibility of an animal taking advantage of a particular habitat (Wang et al., 2008). Vegetation characteristics are often used as indicators of the suitability or quality of small mammal habitats (Jorgensen, 2002). Habitat suitability in different treatments were evaluated from the aspects of productivity, disturbance intensity and habitat shelter. Habitat productivity was defined as the total biomass of plants (i.e., the sum of above ground shrub biomass and herbaceous biomass). Habitat disturbance intensity was measured using stocking capacity, grazing frequency, human activity, and plant diversity in different treatments. Habitat shelter was measured using plant height, coverage and density.

Total biomass and Shannon–Wiener index of plant species, shrub height, and coverage, density and biomass of shrubs and herbaceous plants in different treatments were investigated. These indices were also analyzed by the mixed effects model (Proc mixed, SAS9.2) with a significance level of $\alpha = 0.05$, using Tukey's test for means comparison, with blocks and years set as random effects.

3. Results and analysis

3.1. Habitat suitability

Total plant biomass of the reclamation area was significantly higher than that of the other three disturbed areas [$F_{(3,687)} = 48.91$, $P < 0.001$, Table 2]. Total biomass in the grazing areas were lower than in the grazing exclusion area, although there were no statistically significant differences (Table 2). The nutrition balanced value of *Reaumuria soongorica* was lower than that of other plants (Wu et al., 2010), and *R. soongorica* was not main food for desert rodents in our study area (Wu et al., 2009). There were significant differences in total biomass removed *R. soongorica*, which followed in the order: Grazing exclusion area > light grazing area > heavy grazing area [$F_{(2,513)} = 61.77$, $P < 0.001$, Table 2].

We measured the degree of habitat disturbance using stocking capacity and plant diversity. Stocking capacity in each habitat were described above, and analysis focused on the plant diversity of disturbed habitats. The Shannon–Wiener index of shrubs showed a significant difference among different treatments [$F_{(3,706)} = 280.38$, $P < 0.001$, Table 2].

There were significant differences in height, coverage and density of plants in different treatments. Shrub height followed a significant order: Reclamation area > grazing exclusion area > light grazing area > heavy grazing area [$F_{(3,687)} = 1044.47$, $P < 0.001$, Table 2]. Shrub coverage was highest in the light grazing area, and was lowest was in the heavy grazing area [$F_{(3,687)} = 3.08$, $P < 0.05$, Table 2]. Shrub density in grazing exclusion area was significantly higher than that in light grazing area, heavy grazing area, and reclamation area. Reclamation decreased shrub density significantly than other treatments [$F_{(3,691)} = 68.95$, $P < 0.001$, Table 2]. Herbaceous height was higher significantly in reclamation than that in other treatment areas, while the lowest was in the grazing exclusion area [$F_{(3,691)} = 110.72$, $P < 0.001$, Table 2]. Herbaceous coverage in the

TABLE 2 Vegetation characteristics in different treatments in the Alxa desert, Inner Mongolia, China, from April 2006 to October 2011.

| Indices | Reclamation | Grazing exclusion | Light grazing | Heavy grazing | sem | F-value | P-value |
|--|-------------|-------------------|---------------|---------------|-------|---------|---------|
| Total biomass (g/m ²) | 97.23a | 50.93b | 39.53b | 42.86b | 10.36 | 48.91 | <0.001 |
| Total biomass (remove <i>Reaumuria soongorica</i> biomass) (g/m ²) | — | 50.65a | 24.25b | 8.61c | 5.71 | 61.77 | <0.001 |
| Shannon–Wiener index of plant | 0.22d | 0.91b | 1.07a | 0.38c | 0.03 | 280.38 | <0.001 |
| Shrub height (cm) | 133.22a | 43.72b | 26.67c | 18.80d | 2.08 | 1044.4 | <0.001 |
| Shrub coverage (%) | 15.65ab | 16.64ab | 22.39a | 12.55b | 2.95 | 3.08 | 0.03 |
| Shrub density (plants/m ²) | 0.20c | 0.78a | 0.56b | 0.49b | 0.07 | 68.95 | <0.001 |
| Shrub biomass (g/m ²) | 55.01a | 40.29b | 28.52c | 35.96bc | 7.02 | 12.75 | <0.001 |
| Herbaceous height (cm) | 7.08a | 3.27b | 2.59b | 1.58c | 0.49 | 110.72 | <0.001 |
| Herbaceous coverage (%) | 8.29a | 1.80b | 1.80b | 0.57b | 0.73 | 93.50 | <0.001 |
| Herbaceous density (plants/m ²) | 179.45a | 67.19c | 103.63bc | 123.60b | 23.71 | 17.96 | <0.001 |
| Herbaceous biomass (g/m ²) | 42.22a | 10.64b | 11.02b | 6.90b | 5.76 | 68.90 | <0.001 |

Different letters in columns indicate significant differences ($P < 0.05$) according to Tukey's test. "—": No presence of this species, sem: Standard error of means between treatments.

reclamation area was significantly higher than that in the other three disturbed habitats [$F_{(3,460)} = 93.50$, $P < 0.001$, **Table 2**]. Herbaceous coverage in the grazing exclusion area and light grazing area were higher than that in the heavy grazing area, although there was no significant difference in herbaceous coverage among different grazing habitats.

3.2. Rodent community structure and diversity

We captured 5,129 rodent individuals belonging to nine species, seven genus, and three families in 6 years. There were three species of Dipodidae, including NTJ, MFJ, and MTTJ; five species of Cricetidae, including midday gerbil (MIG, *Meriones meridianus*), Mongolian gerbil (MOG, *Meriones unguiculatus*), desert hamster (DH, *Phodopus roborovskii*), Chinese hamster (CH, *Cricetulus barabensis*), and Eversmann's hamster (EH, *Cricetulus eversmanni*); one species of Sciuridae: Alashan ground squirrel (*S. alaschanicus*). The total capture rates both in grazing exclusion area and light grazing area were significantly higher than that in the reclamation area [$F_{(3,15)} = 13.40$, $P < 0.001$, **Figure 2**]. The reclamation area had a rodent community dominated by MIG [$F_{(4,20)} = 9.48$, $P < 0.001$, **Table 3**]. NTJ and MIG were the dominant species in the grazing exclusion area [$F_{(6,30)} = 10.77$, $P < 0.001$, **Table 3**]. Rodent communities in the light grazing [$F_{(6,30)} = 11.43$, $P < 0.001$] and heavy grazing areas were dominated by NTJ and MFJ [$F_{(8,40)} = 18.78$, $P < 0.001$, **Table 3**].

Species richness in the reclamation area was significantly lower than in the other three treatments [$F_{(3,15)} = 20.76$, $P < 0.001$], but there was no significant difference between the grazing exclusion area, light grazing area and heavy grazing area (**Table 4**). Shannon–Wiener index [$F_{(3,15)} = 10.19$, $P < 0.01$] and Simpson's diversity index [$F_{(3,15)} = 9.09$, $P < 0.01$, **Table 4**] of the rodent community in the reclamation area were significantly lower than in the other treatments. Both indices showed the following order: Grazing exclusion < light grazing < heavy grazing treatment, although the

differences were not statistically significant. The evenness index was not significantly different between the four disturbances (**Table 4**).

3.3. The composition of life history strategists in different disturbed communities

The species richness of *rRF* strategists was significantly greater than that of *KSS* strategists in the reclamation area [$F_{(1,10)} = 19.29$, $P < 0.01$, **Figure 3A**]. Reclamation decreased *KSS* strategists' species richness significantly ($F_{(3,15)} = 58.85$, $P < 0.001$), but did not decrease *rRF* strategists' species richness (**Figure 4A**). *KSS* strategists had higher species richness than *rRF* strategists in the other three treatments, although there was no significant difference between the species richness of *rRF* strategists and *KSS* strategists in the other three treatments (**Figure 3A**).

The proportion of *rRF* strategists was significantly higher than that of *KSS* strategists in the reclamation area [$F_{(1,10)} = 334.86$, $P < 0.001$, **Figure 3B**], while the opposite was the case in the other three areas [grazing exclusion: $F_{(1,10)} = 5.99$, $P < 0.05$, light grazing: $F_{(1,10)} = 14.81$, $P < 0.01$, heavy grazing: $F_{(1,10)} = 54.59$, $P < 0.001$, **Figure 3B**], and the proportion of *KSS*-strategists significantly increased with grazing intensity [$P = 0.034$, 0.003, 0.0001, **Figure 3B**]. The capture rate of *rRF* strategists in the grazing exclusion areas was the highest among all treatments, while the lowest was in the heavy grazing treatment [$F_{(3,15)} = 67.36$, $P < 0.001$, **Figure 4B**]. The capture rate of *KSS* strategists in the reclamation area was the lowest among all treatments [$F_{(3,15)} = 67.35$, $P < 0.001$, **Figure 4B**]. There was no significant effect of grazing on the *KSS* strategist capture rate (**Figure 4B**).

3.4. Rodent community stability

The *W*-statistic values in the reclamation area and heavy grazing area fluctuated greatly, but the fluctuation in the light grazing area and grazing exclusion area were smaller than in the other areas

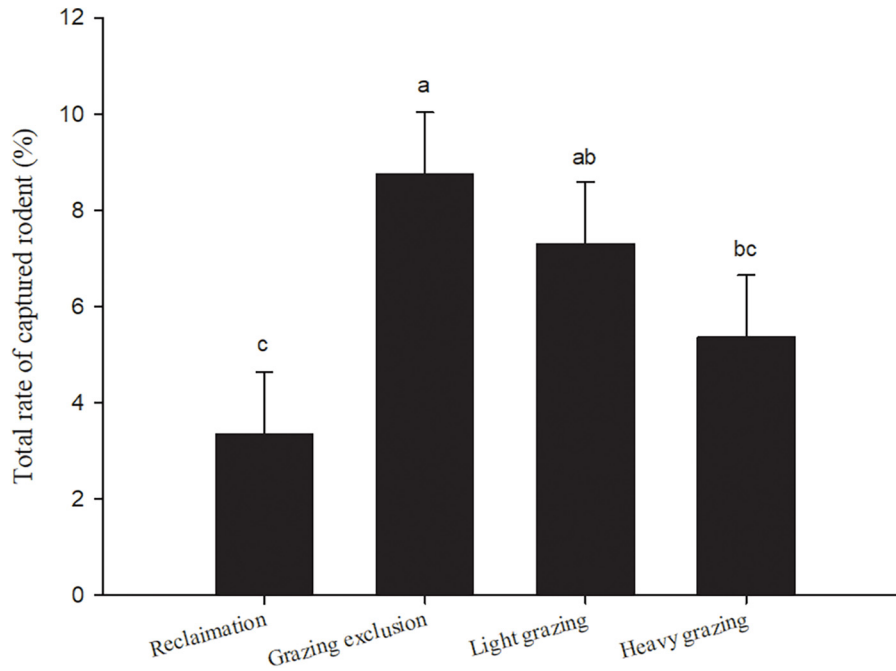


FIGURE 2

Total rate of captured rodents (means + sem) in different treatments in Alxa desert, Inner Mongolia, China, from April 2006 to October 2011. Different lowercase letters indicate significant differences ($p < 0.05$) among treatments, according to Tukey's test.

TABLE 3 Total proportion (%; means + sem) of each rodent species in the rodent community in different treatments in the Alxa desert, Inner Mongolia, China, from April 2006 to October 2011.

| Species | Reclamation | Grazing exclusion | Light grazing | Heavy grazing |
|----------------------------------|-------------|-------------------|---------------|---------------|
| <i>Spermophilus alaschanicus</i> | 7.09b | 4.72cd | 1.97bc | 8.88b |
| <i>Orientallactaga sibirica</i> | 1.14b | 3.17cd | 16.21b | 42.75a |
| <i>Dipus sagitta</i> | — | 53.40a | 52.23a | 30.02a |
| <i>Stylodipus andrewsi</i> | — | — | — | 0.48b |
| <i>Meriones meridianus</i> | 74.07a | 21.47b | 16.48b | 6.16b |
| <i>Meriones unguiculatus</i> | 7.79b | 0.07d | 1.48bc | 4.45b |
| <i>Cricetulus barabensis</i> | 9.92b | 0.18d | 0.16c | 0.05b |
| <i>Cricetulu eversmanni</i> | — | — | — | 0.27b |
| <i>Phodopus roborovskii</i> | — | 16.99bc | 11.49bc | 6.94b |
| Sem | 3.21 | 3.56 | 3.5 | 3.14 |
| F-value | 89.72 | 28.99 | 26.89 | 22.82 |
| P-value | <0.001 | <0.001 | <0.001 | <0.001 |

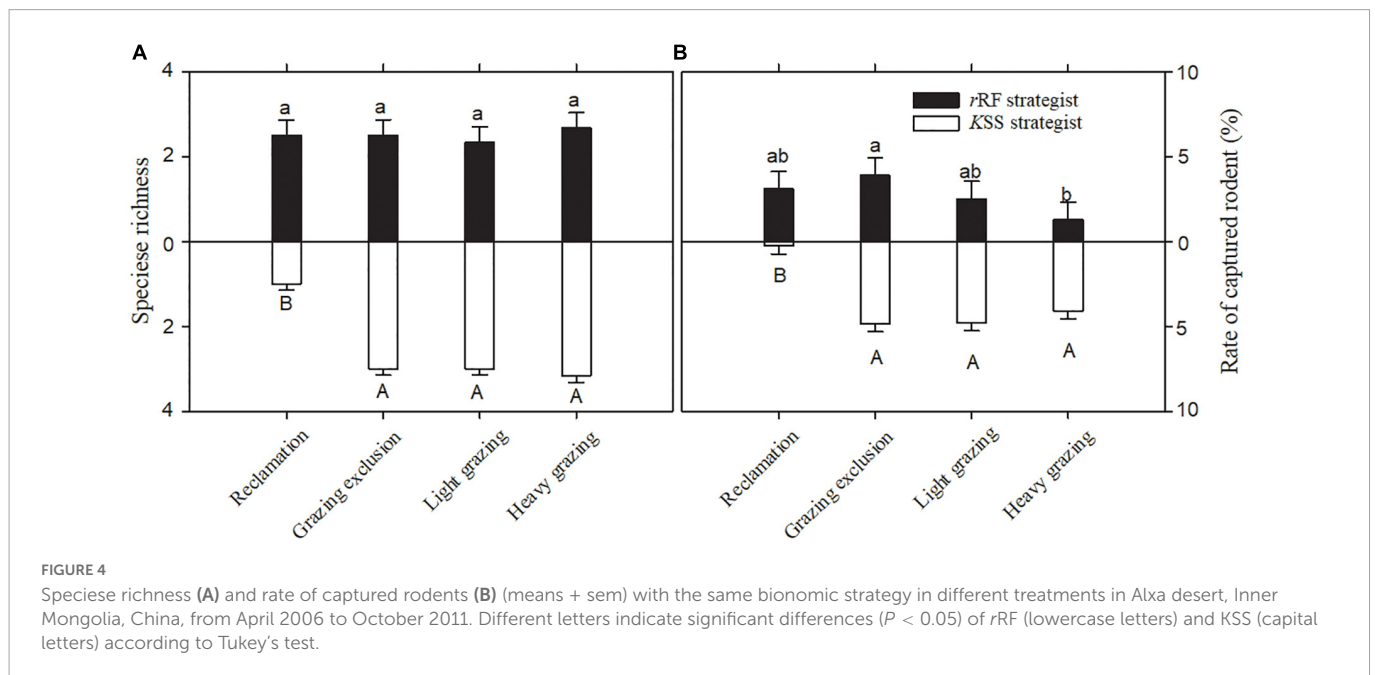
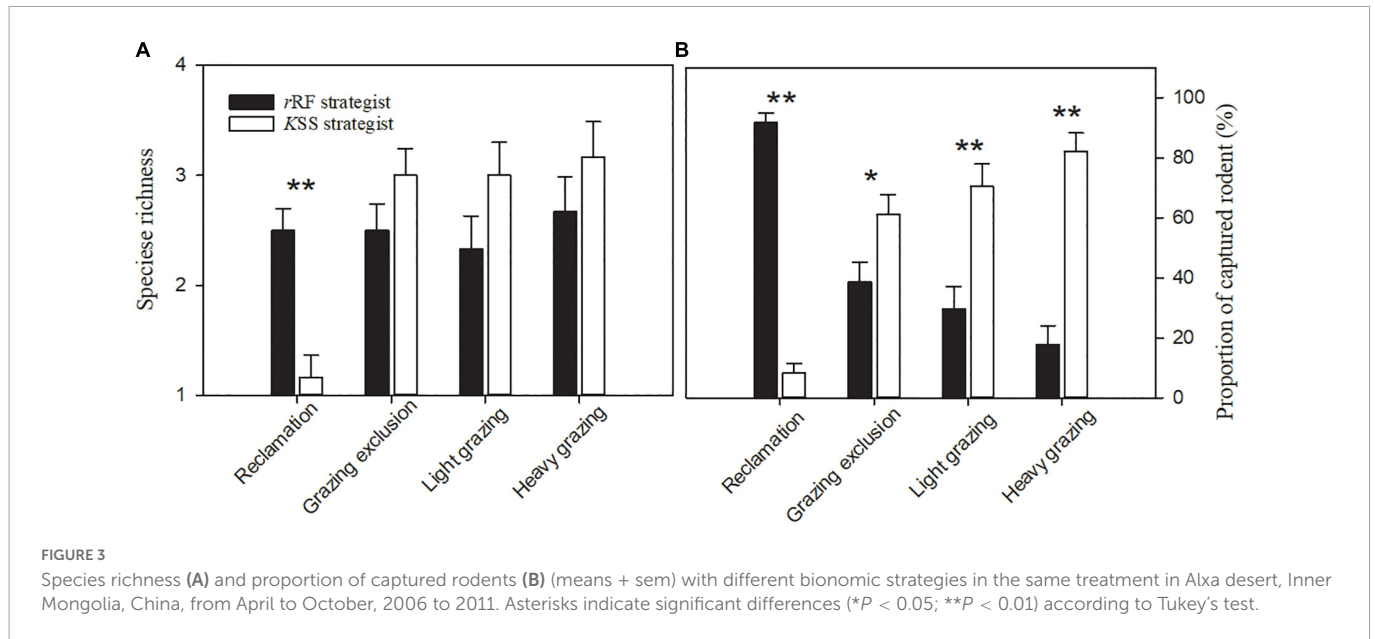
Different letters in rows indicate significant differences ($P < 0.05$) according to Tukey's test.

“—”: No individual of this species was captured, sem: Standard error of means between rodent species.

TABLE 4 Rodent community diversity (means + sem) in different treatments in the Alxa desert, Inner Mongolia, China, from April 2006 to October 2011.

| Diversity indices | Types of disturbance | | | | sem | F-value | P-value |
|---------------------------|----------------------|-------------------|---------------|---------------|------|---------|---------|
| | Reclamation | Grazing exclusion | Light grazing | Heavy grazing | | | |
| Species richness | 3.50b | 5.50a | 5.33a | 5.50a | 0.34 | 20.76 | <0.01 |
| Shannon–Wiener index | 0.76b | 1.14a | 1.18a | 1.31a | 0.09 | 10.19 | <0.01 |
| Pielou evenness index | 0.56a | 0.65a | 0.68a | 0.73a | 0.05 | 2.68 | 0.08 |
| Simpson's diversity index | 0.45b | 0.62a | 0.65a | 0.68a | 0.05 | 9.09 | <0.01 |

Different letters in each row indicate significant differences ($P < 0.05$) according to Tukey's test. sem: Standard error of means between treatments.



(Figure 5). The analysis of variance showed that the W -statistic values in the heavy grazing treatment were significantly higher than that in the reclamation area [$F_{(3,20)} = 4.58$, $P < 0.05$, Figure 5]. The W -statistic value in the reclamation area was less than 0 in most years, but was greater than 0 in most years in the other treatments. The cumulative biomass dominance of the rodent community in the grazing exclusion, light grazing, and heavy grazing treatments were dominated by individual species, while the cumulative abundance dominance of the rodent community was influenced by multiple species. However, the opposite result was observed in the reclamation area (Figure 5).

Regardless of treatment, variability of dominant species richness in all rodent communities was the lowest, while the richness of the non-dominant species showed stronger variability (Table 5). In the grazing exclusion, light grazing and heavy grazing treatments, rodent species with larger body size had a low variation coefficient, and

large variation mainly occurred in rodent species with smaller body size (Table 5). In the reclamation treatment, variability of all rodents was high (>70%, Table 5). *S. andreusi* and *C. evermanni* were rare species in the study sites, with a low capture rate, reflected in greater variability (Table 5). Variability of total abundance in reclamation treatment was the highest (Table 5).

Regarding the community structure of different strategists, variation in the population abundance, and species richness of KSS strategists in the reclamation area was greater than that of *r*RF strategists, but in other treatments the opposite was found (Table 6). The variability of population abundance and species richness of KSS strategists in the grazing exclusion area were the lowest (Table 6). The abundance variability of *r*RF strategists in the heavy grazing area was the highest (Table 6). The species richness variability of *r*RF strategists in the grazing exclusion and light grazing areas were the highest (Table 6). The maximum variation of rodent total abundance

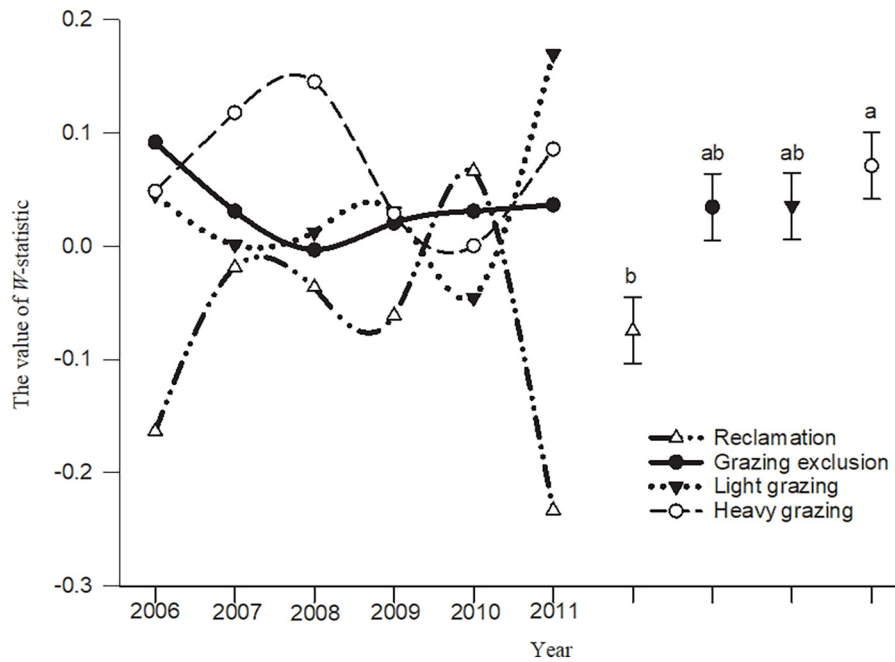


FIGURE 5

W-statistic dynamic and mean comparison (means \pm sem) in different treatments in Alxa desert, Inner Mongolia, China, from April 2006 to October 2011. Different letters indicated significant differences ($P < 0.05$) according to Tukey's test.

was in the reclamation area, while the minimum was in the light grazing sites (Table 6). The maximum variation of total species richness was in the light grazing treatment, while the minimum was in the grazing exclusion treatment (Table 6).

4. Discussion and conclusion

4.1. Habitat suitability

The relationship between stability and disturbance may depend on productivity (Fränze, 1979). The plant productivity of the reclamation area was the highest compared to the other areas. There was no significant difference in productivity among the grazing exclusion areas and grazing areas, but heavy grazing significantly reduced the biomass of plants with higher nutrient value. This indicates that grazing did not affect plant total biomass but did affect plants with high nutritional value. Studies have shown that herbivorous feeders are selective to the forage due to the characteristics of growth and development and nutritional of the plants (Nagaishi and Takemoto, 2018). Some studies have found that livestock in grassland tend to choose high-quality plants rather than plants with low palatability (Peco et al., 2005). Fleischner (1994) also argued that heavy grazing results in a decline in pasture quality, so plant species that are resistant to grazing become dominant. Therefore, our results support the view that livestock grazing affected plant quality rather than plant total biomass. Heavy grazing reduced the shrub height and coverage of plant. Plant diversity indicates that the intensity of interference was the largest in the reclamation area, followed by the heavy grazing area, light grazing area and grazing exclusion area (Table 2 and Figure 6). According to habitat productivity, plant quality and animal shelter, rodents in the heavy

grazing area faced the greatest environmental pressure, followed by the light grazing area, grazing exclusion area, and reclamation area (Figure 6). The intermediate disturbance hypothesis suggests that moderate interference suppresses competitive exclusion of dominant species and thus has a higher diversity than under severe and mild interference (Connell, 1978). There are some evidences from previous studies that moderate disturbance increases rodent diversity in forest ecosystems (Sullivan et al., 2000; Yang et al., 2018, 2022). However, we did not observed higher diversity of rodents in light grazing area, and dominant species was not suppressed under light grazing. These results may be caused by the differences from disturbance type, species in desert ecosystem. Disturbances cause habitat fragmentation, which will reduce the number of species and species diversity (Krishna et al., 2008; Hagen et al., 2012). According to human activities, rodent in reclamation area experience more disturbance from various farming activities than that in grazing area, and the habitat is completely changed, therefore the rodent number and diversity rate at the minimum level in the reclamation area.

4.2. Stability and diversity

In our study, the reclamation area had a significantly lower rodent community diversity. Reclamation reduced community stability by increasing temporal variability of community. The relationship between diversity and stability has been debated for a long time (Hu et al., 2022). The diversity-stability hypothesis suggested that the higher the species diversity in a community, the more stable the community (MacArthur, 1955). May has also argued that simple communities are more stable (May, 1973). However, some scholars believe that these two views are not in conflict. Tilman (1995) suggested that when external interference damages some species, the number of other non-injured species who are competing with the

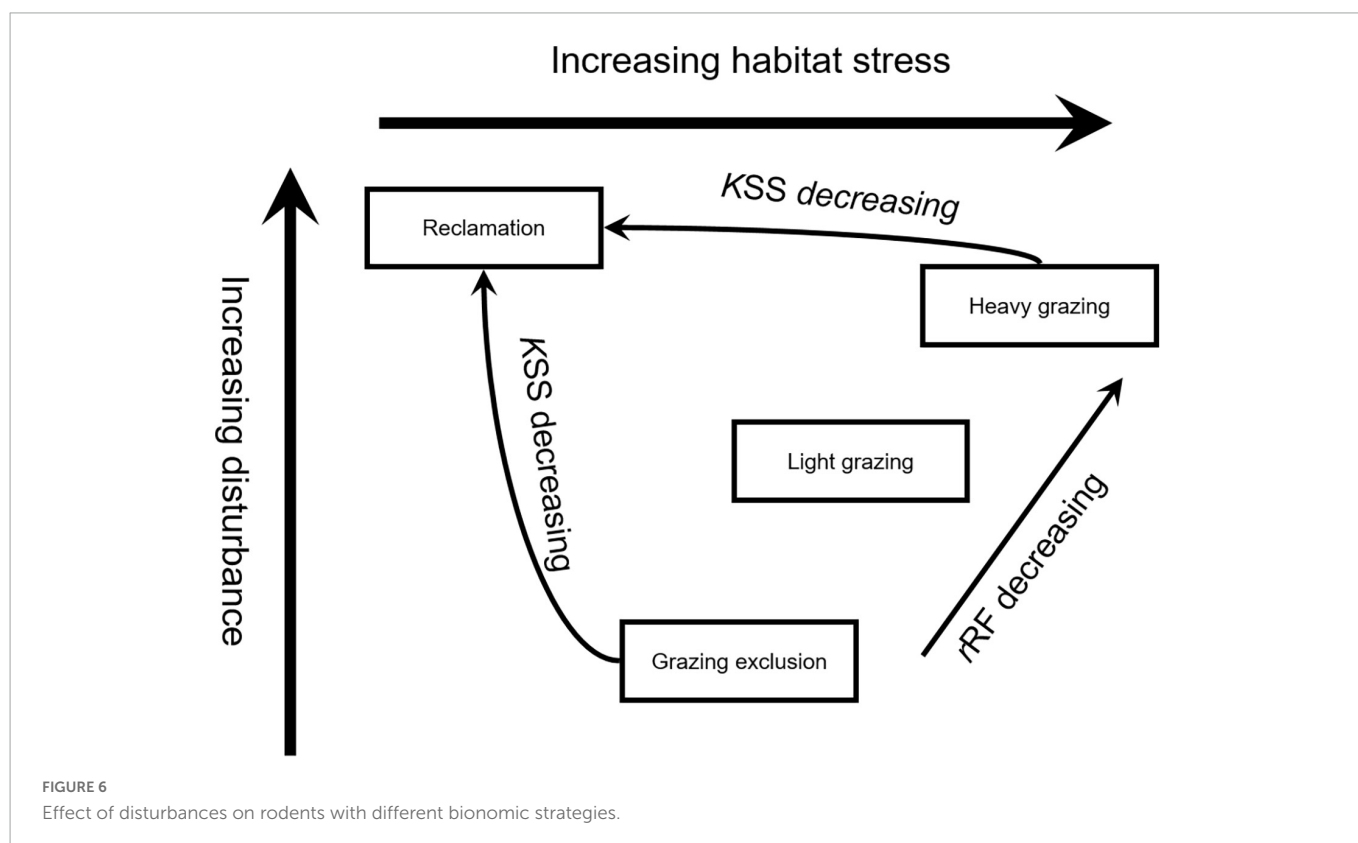
TABLE 5 Variability of rodent populations subjected to different disturbances (%) in Alxa desert, Inner Mongolia, China, from April 2006 to October 2011.

| Species | Reclamation | Grazing exclusion | Light grazing | Heavy grazing |
|----------------------------------|-------------|-------------------|---------------|---------------|
| <i>Spermophilus alaschanicus</i> | 79.59 | 27.70 | 79.63 | 39.19 |
| <i>Orientallactaga sibirica</i> | 244.95 | 52.87 | 37.01 | 21.98 |
| <i>Dipus sagitta</i> | – | 25.08 | 38.19 | 58.24 |
| <i>Stylodipus andrewsi</i> | – | – | – | 244.95 |
| <i>Meriones meridianus</i> | 74.52 | 123.99 | 114.59 | 131.92 |
| <i>Meriones unguiculatus</i> | 137.83 | 244.95 | 244.95 | 178.71 |
| <i>Cricetulus barabensis</i> | 118.98 | 195.10 | 167.33 | 244.95 |
| <i>Cricetulus evermanni</i> | – | – | – | 244.95 |
| <i>Phodopus roborovskii</i> | – | 70.69 | 102.89 | 122.59 |

“–”: Not captured.

TABLE 6 Variability of rodent communities subjected to different disturbances (%) in Alxa desert, Inner Mongolia, China, from April 2006 to October 2011.

| | | Reclamation | Grazing exclusion | Light grazing | Heavy grazing |
|------------------|----------------|-------------|-------------------|---------------|---------------|
| Abundance | KSS strategist | 83.25 | 19.97 | 32.63 | 30.67 |
| | rRF strategist | 72.60 | 89.18 | 96.58 | 124.28 |
| | Σ | 70.80 | 46.38 | 44.33 | 50.51 |
| Species richness | KSS strategist | 63.25 | 0.00 | 14.41 | 12.89 |
| | rRF strategist | 21.91 | 55.78 | 55.78 | 38.73 |
| | Σ | 15.65 | 15.21 | 19.36 | 16.85 |



injured species in the community will increase. This compensation can increase community total biomass stability, but also cause variation in species abundance. He argued that this conclusion not only supported May’s consideration of the impact of diversity on the population, but also applied the diversity-stability hypothesis

to community and ecology processes. McCann (2000) showed that diversity usually contributes to stability, but that diversity is not the driving force of stability. Grazing did not make significant difference in the diversity of rodent community, but, changed the dominant species among different grazing disturbances. The effect

of grazing on the rodent community stability may come from the response of species or functional groups with different responsiveness to disturbances (de Valpine, 2000). Life history characteristics are often used as the main indicators of community functional (Kirwan et al., 2009; Rodríguez and Ojeda, 2014; Lin et al., 2022). Functional stability was one of the important aspects of stability in ecological communities (Huelsmann and Ackermann, 2022).

From the habitat suitability and the characteristics of different strategists, we can understand the different changes in the reclamation and grazing areas among different strategists. For animals, habitat shelter has an important impact on habitat selection, and predation risk may result in the specialization of smaller mammals in habitats with excellent shelter. The reclamation areas with high shrub height, herbaceous height, herbaceous coverage, and herbaceous density, these conditions provided excellent shelter for *rRF* strategists with small body size (Cui et al., 2005). On the other hand, *rRF* strategists with a higher reproductive rate and a longer reproductive period, which is beneficial to increase the population in a short time. Studies have shown that when habitat heterogeneity occurs and the original ecosystem becomes less stable, a higher population size is better able to cope with the impact of heterogeneity (Shadrina and Vol'pert, 2016). Above, we can understand the changes in the reclaimed areas among different strategists. Grazing areas have higher biodiversity than reclaimed areas, which means they have higher stability. How do these communities acquire the stability in response to disturbances? It is universally acknowledged that increase in animal body size reduces environmental resistance in many ways. It maybe that there is an increase in the number of *KSS* strategists in the community, the increased resistance of the community. In our study, our proposed hypothesis was verified. At the same time, our research may answer these three questions from the respect of life history strategy. From a diversity perspective, the ecosystems with intermediate disturbance are more stable, in other words, with higher resilient and resilient.

4.3. Stability and resistance, resilience, and variability

McNaughton (1977) argued that species with different adaptation patterns, whose abundance is volatile, may be a mechanism for the community to remain stable in a volatile environment. The adaptation patterns here were likely to be related to life history strategies of the species (McNaughton, 1977). Studying how different systems are dominated by animals with different life history strategies can help us solve the problem of resistance and resilience (Pimm, 1984).

Pianka (1970) argued that increase in animal body size reduces environmental resistance in many ways. Animals with larger body size have fewer potential predators, and more adaptable to the environment (Meador and Brown, 2015). The creatures living longer than 1 year have to deal with physical or biological conditions of the whole range in order to survive, while those living less than 1 year will only experience part of that range during their short- life time. So animals with longer longevity and larger size can better buffer changes in the environment, and their population is not subject to such dramatic change as relatively smaller and shorter-lived animals. A stable population also provides the necessary conditions for a

stable community. Studies in the same study area have shown that the survival rate of the large jerboas is less affected by grazing than *MIG* which is smaller in size (Yuan, 2013). Mammals with a fast strategy have relatively higher reproductive elasticity and lower adult survival elasticity, while mammals with a slow strategy have lower reproductive elasticity and higher adult or juvenile survival elasticity. Since the decline in adult survival is not conducive to the slow strategy mammalian population, the resilience of the slow strategist will be slower once the outside interference exceeds its ability to resist environmental resistance (Heppell et al., 2000). MacArthur and Wilson (1967) argued that high-fecundity strategists can recover from frequent density independent deaths through higher population growth rates. Therefore, *KSS* strategists have higher resistance and lower resilience to external environmental changes. The *rRF* strategists have lower resistance and higher resilience to external environment changes (MacArthur and Wilson, 1967; Pianka, 1970; Heppell et al., 2000). Lepš et al. (1982) argued that two different aspects of stability may be determined by life strategy and external variables of the dominant species. The increase in *KSS* strategists in a community imply an increase in community resistance, whereas an increase in *rRF* strategists implies an increase in community resilience. Variability in community stability reflects the effect of external variables on the community (Lepš et al., 1982). In our study, the reclamation disturbance significantly reduced species richness, the capture ratio, and the capture rate of *KSS* strategists. Therefore, reclamation had a significant negative effect on *KSS* strategists, so the reclamation area had lower community resistance. The resistance variability of rodent community in reclamation was also greater than in the other three disturbed areas. So reclamation reduced rodent community resistance. With an increase in grazing intensity, the capture rate of *KSS* strategists and *rRF* strategists showed a downward trend, and the declining trend of *rRF* strategists was more significant, which caused the dominant advantage of *KSS* strategists in the community to gradually increase. The results from *W*-values also indicate that *KSS* strategists in the grazing exclusion area and grazing areas were dominant, particularly in the heavy grazing treatment. So grazing has a greater impact on *rRF* strategists than on *KSS* strategists (Figure 6). Because the heavy grazing area had lower *rRF* strategy abundance than the other treatments, the heavy grazing area had lower community resilience, and resilience variability was higher than in the other three disturbed regions. There was no significant difference in species richness and population abundance for *KSS* strategists among the heavy grazing area and other areas, and the variability of this resistance was not markedly different among the other three disturbance treatments, so the effect of grazing on community resistance was not significant. Because the heavy grazing area had a lower *rRF* strategist abundance than the grazing exclusion area, so the heavy grazing area had lower community resilience, and resilience variability was larger than in the other two disturbed areas. Therefore, grazing reduced community resilience.

In summary, the increase of *KSS* strategists means the increase of resistance of the community. The increase of *rRF* strategists means the increase of community resilience. Reclamation reduced rodent community stability by increasing temporal variability of community, reducing rodent community resistance as shown by decreasing dominance of *KSS* strategists, and increased the resistance variability of the rodent community by increasing the variability of abundance and richness for *KSS* strategists. Grazing reduced rodent community resilience by reducing the dominance of *rRF* strategists, and increased

the resilience variability of the rodent community by increasing the variability of abundance and richness for *r*RF strategists. Despite the limitations of the theory and data analysis, these findings enhance the understanding of the structure and resilience of ecosystems. Sensitivity to disturbances varies between species, so it is difficult to further explain the hidden mechanisms behind this response (Ma et al., 2004). However, some insights can be gained if sensitive species are classified in terms of bionomic strategy, as this helps elucidate which kind of bionomic strategy sensitive species take when subject to varying disturbances.

Data availability statement

The datasets analyzed for this study can be found in the Science DB: <https://doi.org/10.57760/sciencedb.07040>.

Ethics statement

This animal study was reviewed and approved by the Research Ethics Review Committee of Inner Mongolia Agricultural University (NND2017012).

Author contributions

SY, H-PF, and X-DW designed the experiments and mapped out the manuscript. SY analyzed the data and wrote the initial draft of the manuscript. H-TZ, XL, and X-XY were responsible for the majority of data collection and assisted with revisions of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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